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Preface – Laudatio of Professor Pavel Štys

The present issue of *Acta Societatis Zoologicae Bohemicae* is dedicated to Dr. Pavel Štys, Professor of Entomology and Head of the Department of Zoology at Charles University in Prague, on occasion of his 65th birthday, and in honour of his lifetime entomological studies.

Professor Pavel Štys is an eminent researcher of the insect order Heteroptera, as seen by heteropterists from all over the world. He has published nearly four hundred works of different types. Scientific papers represent more than 170 publications, books, book chapters or textbooks about 25. The majority of his publications deal with alpha- or beta taxonomy, morphology, ecology, ethology, bionomics, ontogeny, paleontology, zoogeography, phylogeny, and faunistics, either of various heteropteran taxa, at all taxonomic levels, or of the order Heteroptera as a whole.

Professor Štys was engaged also in other taxa of Insecta, during the beginning of his scientific career, for example, he studied the family Syrphidae from the order Diptera.

Later on, he devoted his attention also to some questions about the phylogeny and higher classification of the arthropod superclass Hexapoda, and other various taxa from the phylum Arthropoda.

A scientific scope of Professor Štys includes even the problems of theoretical entomology, comparative morphology, phylogeny of animals in general, and evolutionary biology. Most of his results and conclusions are widely accepted and frequently mentioned and quoted by the other scientists.

It is clearly evident, from a short telegraphic survey, that Professor Štys is a versatile and at present time already rare "renaissance personality", with a wide scientific interest, extensive publication activity, and high productivity. The results of his research has enlarged the human knowledge significantly.

The proof of a high estimation of Professor Štys's research is, among others, even his membership in a number of Czech, foreign, and international scientific societies, committees, boards, and institutions, e. g., American Entomological Society, Society of Systematic Zoology, Scientific Board of Institute of Entomology of the Czech Academy of Sciences, Editorial Board of *European Journal of Entomology*, Czech Committee IUBS at Czech Academy of Sciences; nomination as Research Fellow of the American Museum of Natural History in New York.

Professor Štys's position as an university teacher at Charles University is not of less importance. Besides teaching of graduate courses of General Entomology, Insect morphology and



***Cryptovelia stysi* sp. n. from Borneo with a reanalysis of the phylogeny of the Mesoveliidae (Heteroptera: Gerromorpha)**

Nils Møller ANDERSEN

Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark

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Abstract *Cryptovelia stysi* sp. n. is described from Malaysian Borneo (Sarawak). This is the second species known in the genus which comprise tiny, almost eye-less bugs living in the moist soil-litter layer of tropical rainforests in Brazil and Borneo. The results of a cladistic analysis of between the genera of Mesoveliidae are presented. Finally, the zoogeographical implications of the distribution of mesoveliid bugs are discussed briefly.

Taxonomy, new species, cladistic analysis, zoogeography, Heteroptera, Gerromorpha, Mesoveliidae, world-wide fauna

INTRODUCTION

Semiaquatic bugs (Heteroptera, infraorder Gerromorpha) are distributed world-wide with about 1,600 described species. The group includes the familiar water striders or pond skaters which are conspicuously adapted to life on the surface film of water (the pleustonic zone) in both limnic and marine habitats. Several groups of gerromorph bugs, however, live in various humid terrestrial and marginal aquatic habitats (the hygropetric zone). Previous ideas about the ecological evolution of semiaquatic bugs (e. g., China 1955) suggested an early colonization of the water surface by "littoral" bugs (the Saldidae or shore bugs were thought to be the sister group of the Gerromorpha). These bugs included the ancestor of all families except the Mesoveliidae and Hebridae. Terrestrial or hygropetric forms of the families Macroveliidae and Hydrometridae were seen as examples of secondary return to land.

I dedicate the present work to Prof. Pavel Štys in recognition of his outstanding contribution to our knowledge about the comparative morphology, phylogeny, and higher classification of the Heteroptera or true bugs. Pavel Štys was among the first workers to question the above mentioned scenario of adaptive evolution in the infraorder Gerromorpha (Štys 1976). His thorough observations and eminent logic of thinking have inspired the author's subsequent work on the classification, phylogeny, and ecological evolution of semiaquatic bugs (Andersen 1979, 1982, 1995b). In this paper, I describe the second species of the genus *Cryptovelia* belonging to the family Mesoveliidae. Species of this genus are tiny, almost eye-less bugs which live in the moist soil-litter layer of tropical rainforests in Brazil and Borneo. Next, the phylogenetic relationships between the genera of Mesoveliidae are reanalyzed using cladistic methods. Finally, the zoogeographical implications of the distribution of mesoveliid bugs are discussed.

TAXONOMY

Cryptovelia Andersen et Polhemus, 1980

Cryptovelia Andersen & Polhemus, 1980: 369–371.

Type-species: *Cryptovelia terrestris* Andersen et Polhemus, 1980; by original designation and monotypy.

DIAGNOSIS AND DESCRIPTION. Very small, 1.1–1.3 mm long, apterous insects, with pale brownish or yellowish ground colour. Head elongate with subparallel sides (Fig. 9), slightly longer than wide across eyes; head length longer than middorsal length of thorax; head slightly declivant in lateral view (Fig. 2) with a transverse ridge at base of head. Ocelli absent. Three pairs of long cephalic trichobothria (Fig. 2, ct) situated almost equidistant on the dorsal head surface; two anterior pairs inserted on swellings. Eyes vestigial, each composed of 3–4 large ommatidia (Figs 2 and 9, oc). Antennal tubercles moderately prominent, situated near apex of head; antennae slender and long, subequal to or slightly shorter than body, flagelliform (Figs 1 and 8); first and third segments subequal in length and fourth segment 2–2.7× as long as first segment; third and fourth segment almost thread-like. Ventral region of head with a pair of low, longitudinal ridges; ventral lobes or bucculae small. Rostrum very long and slender (Fig. 2, ro), apex reaching basal third or half of abdominal sternum; first and second labial segments very small; third segment swollen at base and distinctly tapering in width towards apex, 2.3–4× as long as fourth segment.

All three thoracic segments visible from above as transverse plates with nearly straight or slightly curved intersegmental sutures (Figs 1 and 8). Pronotum (pn) and mesonotum (ms) subequal in length, metanotum (mt) shortest. No trace of wings. The three thoracic pleura almost equal in size (Fig. 2), only distinctly separated from each other in ventral parts. Sternum of thorax and basal abdominal segments faintly carinated in middle. Metathoracic scent orifice inconspicuous, located on elevated posterior part of metasternum. Legs slender and long, hind leg longest. Coxae, including the posterior pair, relatively short (Fig. 2), inserted close to the ventral midline of thorax. Femora without dark spine-like hair along anterior margin; hind tibia without dark spines. Tarsi with three segments; first segment shortest, second segment subequal to or slightly shorter (fore and middle leg), or slightly longer than third segment (hind leg). Claws slender, inserted apically on last tarsal segment; dorsal arolium feather-like, ventral arolium bristle-like.

Abdomen broad, length subequal to or slightly more than greatest width. Mediotergites tapering in width towards abdominal apex; a small scent orifice situated in middle of tergite 4 (Fig. 8, so). Laterotergites (connexiva) relatively broad, slightly raised. Male genital segments relatively small but distinctly visible from above (Fig. 1). Segment 8 rectangular (Fig. 3), pygophore (segment 9) subovate (Figs 2, 4–5, py); proctiger (pr) narrow, with or without lateral modifications; parameres small, symmetrical (Figs 4–5 and 7, pa). Female genital segments large (structural details, see Andersen & Polhemus 1980: figs 13–14). First gonocoxa (= segment 8) plate-shaped (Fig. 10, gx1); first gonapophyses elongate, lacinate, with small teeth on inner margin in distal part; gonangulum and tergum 9 (t9) well developed, proctiger (pr) small and cone-shaped. Second gonocoxa plate-shaped; gonoplares (Fig. 10, gp) relatively small; second gonapophyses weakly sclerotised, elongate with pointed apices.

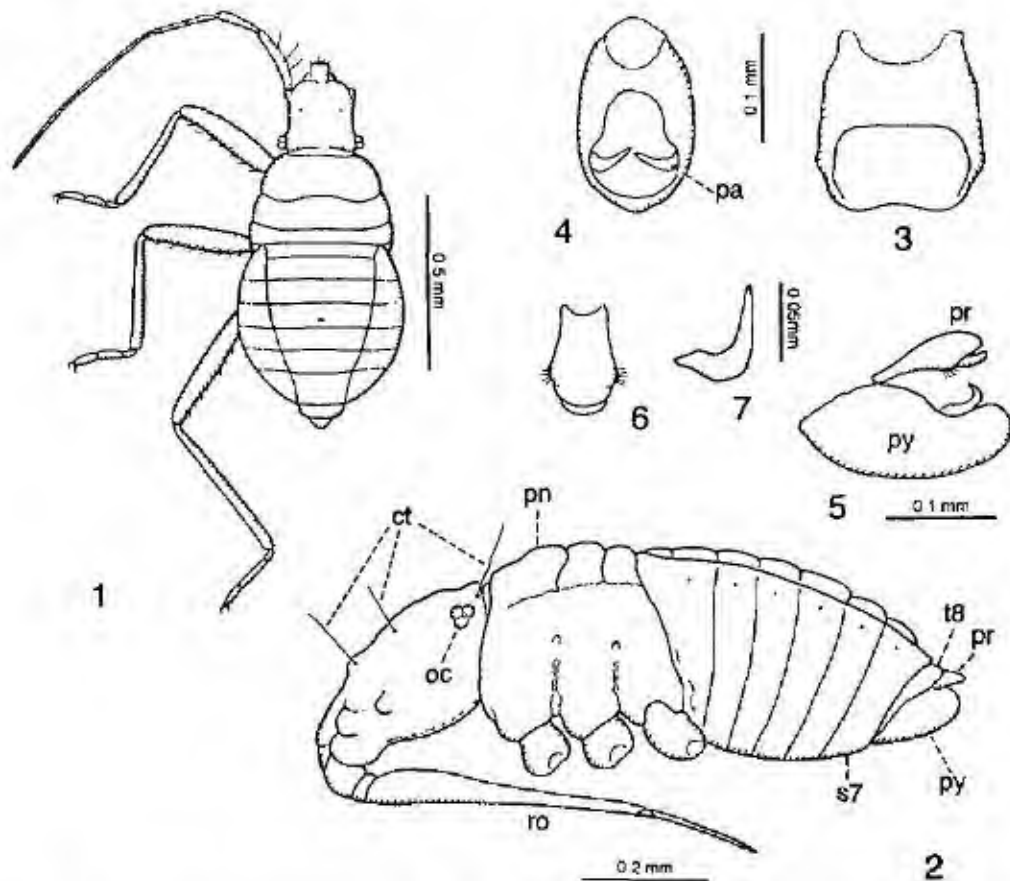
Macropterous adult form unknown.

DISTRIBUTION. Neotropical (Brazil) and Oriental Region (Borneo) (see map, Fig. 12).

***Cryptovelia terrestris* Andersen et Polhemus, 1980**

Cryptovelia terrestris Andersen et Polhemus, 1980: 371–373, figs 1–18.

MATERIAL EXAMINED. **Holotype:** apterous male, labelled: "Brazil, Pará, 5 km E. Belém, Apr. 26, 1974, soil-litter layer in primary forest, Leg. R. T. Schuh". Holotype deposited in Museu Nacional, Rio de Janeiro, Brazil. **Paratypes** BRAZIL: 1 male, 1 female (apterous), Pará, 8 km E. Belém, Ananindeua, May 22 & June 30, 1973, litter in high secondary forest, R. T. Schuh; 1 female (apterous), Pará, 5 km E. Belém, May 30, 1973, soil-litter layer in primary "terra firme" forest, R. T. Schuh. All deposited in the Zoological Museum, University of Copenhagen, Denmark. Other paratypes deposited in the American Museum of Natural History, New York, and in the J. T. Polhemus Collection, Englewood, Colorado (property of the National Museum of Natural History, Washington, D.C.), all in U.S.A. (for details see Andersen & Polhemus 1980).



Figs 1–7. *Cryptovelia terrestris* sp. n., apterous male. 1 – dorsal view, appendages of right side omitted; 2 – lateral view, antenna and legs except coxae omitted; 3 – segment 8, ventral view; 4 – pygophore (segment 9), dorsal view; 5 – pygophore and proctiger, lateral view; 6 – proctiger, dorsal view; 7 – left paramere. Abbreviations: ct, cephalic trichobothria; oc, eye; pa, paramere; pn, pronotum; pr, proctiger; py, pygophore (segment 9); ro, rostrum; s7, sternum 7; t8, segment 8.

REDESCRIPTION Size Apterous male, length 1.2–1.3 mm, greatest width (across metathorax) 0.50–0.52 mm, apterous female, length 1.2–1.3 mm, greatest width (across abdomen) 0.52–0.56 mm.

Colour and vestiture Body above brownish-yellow, dull. Head yellowish and chiefly dull, with a darker spot anteriorly between antennal tubercles. Antennae, rostrum, legs, and ventral surfaces of thorax and abdomen, pale yellowish. Body and legs with pale semierect pubescence.

Structure, apterous male (units of measurements, 1 unit = 12.5 μ m). Head length subequal to width across eyes (24:20) with a sharply demarcated, transverse ridge at base of head, anterior part of head broadly depressed between the antennal tubercles. Eyes vestigial, each composed of 3–4 large ommatidia. Antenna distinctly shorter than total body length (80:98), relative lengths of antennal segments: first 18, second 8, third 18, and fourth 36. Rostral apex reaching basal third of abdominal sternum, relative lengths of third and fourth labial segments 36:10.

Dorsal thorax slightly longer than head length (30:24), with evenly rounded sides. Relative lengths of thoracic segments: pronotum 12, mesonotum 12, and metanotum 6, hind margin of pro- and mesonotum slightly sinuate, that of metanotum nearly straight. Relative lengths of leg segments: fore femur 30, fore tibia 26, and fore tarsus 10, middle femur 30, middle tibia 28, and middle tarsus 10, hind femur 38, hind tibia 40, and hind tarsus 16. Fore femur slightly more incrassate than middle femur, middle femora with two prominent, erect and dark spines ventrally. First tarsal segment always shortest (2–3), second segment subequal to third segment in fore and middle tarsus (3:5), subequal to each other in hind tarsus (6:6).

Abdomen about 1.5 \times thorax length (42:30), with broadly rounded. Male genital segments small, but distinctly protruding from the pregenital abdomen. Segment 8 rectangular, with dorsal hind margin emarginate and ventral hind margin straight, pygophore subovate with a lateral notch and group of spines at the points of attachment of parameres, proctiger narrow, with short lateral lobes furnished with groups of stout spines, parameres small, rounded, with short recurved apices.

Structure, apterous female Head longer than wide across eyes (24:21). Relative lengths of antennal segments: first 16, second 9, and third 17 (fourth segment incomplete). Rostral apex reaching anterior third of abdominal sternum, relative lengths of third and fourth labial segments 35:13. Other structures of head as in male.

Dorsal thorax subequal in length to head length (25:24). Relative lengths of thoracic segments: pronotum 11, mesonotum 4.5, and metanotum 2.5, hind margins of pro- and mesonotum slightly curved in middle, that of metanotum nearly straight. Relative lengths of leg segments: fore femur 26, fore tibia 25, and fore tarsus 12.5, middle femur 27, middle tibia 26, and middle tarsus 13, hind femur 32, hind tibia 35, and hind tarsus 14.5. Middle femora without spines. First tarsal segment shortest, second segment shorter than third segment in all tarsi. Other structures of head as in male.

Abdomen much longer than thorax (48:25), distinctly widened across middle with broadly rounded sides. Female genital segments and gynatrial segments illustrated by Andersen & Polhemus (1980: figs 13–16).

DISTRIBUTION Only known from the type series from Brazil (Par ) (see map, Fig. 12).

Cryptovelia stylis sp. n.

(Figs 1–10)

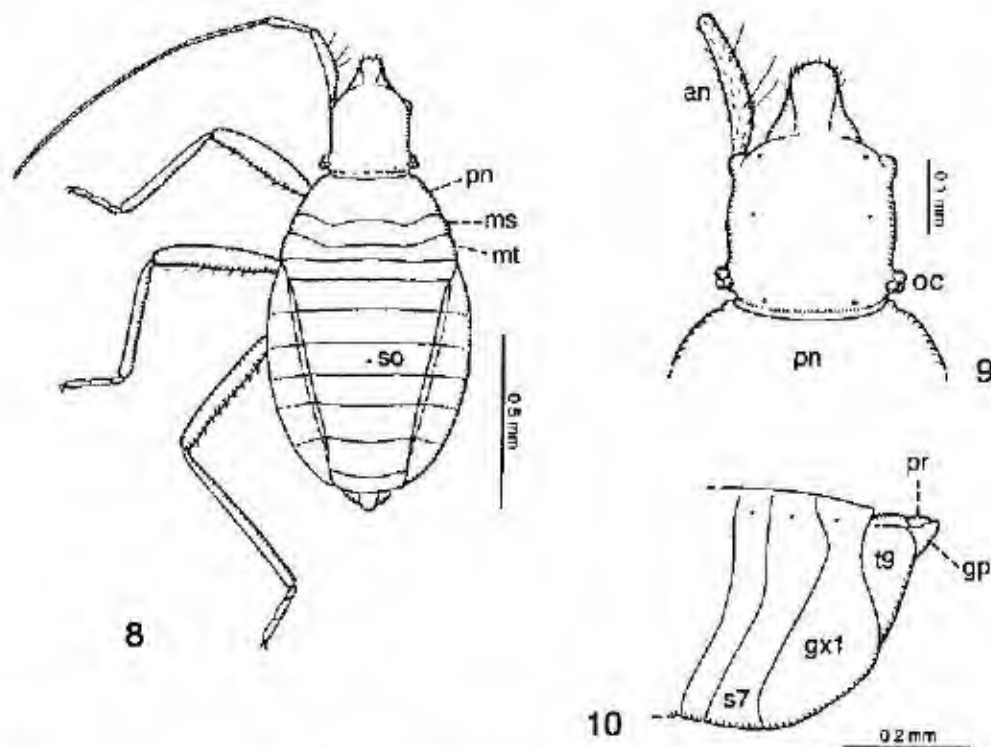
TYPE MATERIAL Holotype: apterous male, labelled "SARAWAK, Kampong Segu, 20 mi [= 30 km] SW of Kuching, rainforest, 4 vi 1968", "leafmould berlesate, RWT-68 291, rainforest", and "R. W. Taylor Accession 68". Deposited in the Australian National Insect Collection, CSIRO Division of Entomology, Canberra A.C.T., Australia. **Paratypes** MALAYSIA (SARAWAK): 15 males, 6 females (apterous), and 2 nymphs, same label data as holotype. Deposited with the holotype and in the Zoological Museum, University of Copenhagen, Denmark.

DESCRIPTION. Size. Apterous male, length 1.0–1.1 mm, greatest width (across abdomen) 0.41–0.45 mm; apterous female, length 1.3–1.4 mm, greatest width (across abdomen) 0.60–0.63 mm.

Colour and vestiture. Ground colour of body pale brownish or yellowish; appendages pale yellowish (specimens of the type series probably bleached as the result of prolonged storage in alcohol). Body and appendages covered by a sparse pubescence of pale, semierect hairs.

Structure, apterous male (units of measurements, 1 unit = 12.5 μ m) (Fig. 1). Head slightly longer than wide across eyes (22:19). A sharply demarcated, transverse ridge at base of head. Eyes vestigial, reduced to 3 large ommatidia (Fig. 2, oc); interocular width of head only slightly smaller (15.5) than width across eyes. Antenna subequal in length to total body length (85:86); relative lengths of antennal segments: first 16, second 9, third 17, and fourth 43. Rostrum very long and slender, its apex reaching middle of abdominal sternum (Fig. 2, ro); relative lengths of third and fourth labial segments 35:14.

Dorsal thorax slightly shorter than head length (18:22), with evenly rounded sides. Relative lengths of thoracic segments: pronotum 9, mesonotum 6, and metanotum 3; hind margin of pronotum slightly curved in middle, those of meso- and metanotum nearly straight. Relative lengths of leg



Figs 8–10. *Cryptovelia styri* sp. n., apterous female. 8 – dorsal view, appendages of right side omitted; 9 – head, dorsal view, antenna except first segment of left side omitted; 10 – abdominal end, lateral view. Abbreviations. an, first antennal segment, oc, eye, gx1, first gonapophysis, ms, mesonotum, mt, metanotum, pn, pronotum, pr, protuber, so, abdominal scent orifice on tergite 4, s7, sternum 7; t9, tergum 9.

segments: fore femur 29, fore tibia 27, and fore tarsus 13; middle femur 24, middle tibia 26, and middle tarsus 12; hind femur 32, hind tibia 36, and hind tarsus 15. Fore femur slightly more incrassate than middle femur; hind femur more slender than other femora; femora and tibia without prominent spinous hairs. First tarsal segment always shortest (2.5–3); second segment subequal to third segment in fore tarsus (5:5), slightly shorter in middle tarsus (4.5:5), longer than third segment in hind tarsus (7:5).

Abdomen about twice as long as thorax (36:18), distinctly widened across middle with broadly concave sides; first abdominal mediotergite short (3.5), tergites 2–7 subequal in length (5–5.5). Male genital segments relatively small (Fig. 2). Segment 8 (Fig. 3) rectangular; pygophore subovate (Figs 4–5); proctiger narrow (Figs 5–6), anteriorly with a group of hairs on lateral margins; parameres small, falciform (Figs 4–5 and 7, pa) with apices pointing mesad.

Structure, apterous female (Figs 8–10). Head distinctly longer than wide across eyes (29:21); each eye with three large ommatidia (Fig. 9, oe); interocular width of head only slightly smaller (17) than width across eyes. Antenna slightly shorter than total body length (99); relative lengths of antennal segments: first 18, second 10, third 19, and fourth 52. Rostrum very long and slender, its apex reaching middle of abdominal sternum; relative lengths of third and fourth labial segments 44:14. Other structures of head as in male.

Dorsal thorax distinctly shorter than head length (18.5), with evenly rounded sides. Relative lengths of thoracic segments: pronotum 10.5, mesonotum 5.5, and metanotum 2.5; hind margins of pro- and mesonotum slightly curved in middle, that of metanotum nearly straight. Relative lengths of leg segments: fore femur 29, fore tibia 27, and fore tarsus 13; middle femur 30, middle tibia 28, and middle tarsus 12.5; hind femur 36, hind tibia 39, and hind tarsus 18. First tarsal segment always shortest (3); second segment subequal to third segment in fore tarsus (5:5), slightly shorter in middle tarsus (4.5:5), longer than third segment in hind tarsus (9:6). Other structures of legs as in male.

Abdomen much longer than thorax (53), distinctly widened across middle with broadly concave sides; first abdominal mediotergite short (4), tergites 2–5 subequal in length (5–7), tergites 6–7 slightly longer (8). Female genital segments relatively large (Fig. 10). First gonocoxae (gx1) large, plate-shaped; proctiger (pr) small, visible from above.

Structure, nymphs. Two nymphs (probably last instar) measuring 0.99 and 1.10 mm, respectively. Colour pale yellowish. Head structure as in adult, each eye with 3 large ommatidia. Pronotum about twice as long as mesonotum. All tarsi with only one segment.

DISTRIBUTION. Malaysia (Sarawak) (see map, Fig. 12).

DIFFERENTIAL DIAGNOSIS. *Cryptovelia stysi* sp. n. can be distinguished from the type species of the genus, *C. terrestris*, by the following characters:

- (1) Head distinctly longer than dorsal length of thorax in *C. stysi* sp. n.; subequal to or shorter than dorsal length of thorax in *C. terrestris*.
- (2) Fourth antennal segment almost three times as long as first segment in *C. stysi* sp. n.; only about twice as long as first segment in *C. terrestris*.
- (3) Apex of rostrum reaching middle of abdominal sternum in *C. stysi* sp. n.; only reaching anterior third of abdominal sternum in *C. terrestris*.
- (4) Pronotum distinctly longer than mesonotum in *C. stysi* sp. n.; subequal to mesonotal length in *C. terrestris*.
- (5) Middle femora of male *C. stysi* sp. n. not modified; with two prominent, erect dark spines on ventral margin in *C. terrestris*.
- (6) Abdomen broad, almost ovoid in dorsal view in *C. stysi* sp. n.; narrower in *C. terrestris* (in particular in males).

- (7) Proctiger of male not modified on lateral margins in *C. styxi* sp. n., with a pair of lateral extensions furnished with stout spines in *C. terrestris*
 (8) Parameres slender and falciform in *C. styxi* sp. n., broad and stout in *C. terrestris*

PHYLOGENY AND CLASSIFICATION

Taxa

The Mesovelidae is one of the smallest of the gerromorphan families. The check-list of Andersen & Polhemus (1980: 389–390) enumerates 9 genera with 32 described species: *Madeovelia* Poisson, 1959, *Mesoveloides* Hungerford, 1929 (Madeoveliinae), *Cavaticovelia* Andersen et Polhemus, 1980, *Cryptovelia* Andersen et Polhemus, 1980, *Darwinivelia* Andersen et Polhemus, 1980, *Mesovelia* Mulsant et Rey, 1852, *Mniovelia* Andersen et Polhemus, 1980, *Phrynovelia* Horváth, 1915, and *Speovelia* Esaki, 1929 (Mesoveliinae). Since then the following new taxa have been added: the genus *Austrovelia* Malipatil et Monteith, 1983, with the species *A. queenslandica* Malipatil et Monteith, 1983, from northern Queensland, Australia, and *A. caledonica* Malipatil et Monteith, 1983, from New Caledonia; the genus *Nereivelia* Polhemus et Polhemus, 1989, with the species *N. murphyi* Polhemus et Polhemus, 1989, from Thailand; *Darwinivelia polheimi* Carvalho, 1984, from Brazil and *D. angulata* Polhemus et Manzano, 1992, from Colombia; *Phrynovelia caledonica* Malipatil et Monteith, 1983, and *P. bimaculata* Malipatil et Monteith, 1983, from New Caledonia; *Mesovelia egorovi* Kanyukova, 1981, from Sakhalin, Far East of Russia, and *M. polheimi* Spangler, 1990, from Belize. This increases the number of mesovelid genera to 11 and the number of described species to 42 (including *Cryptovelia styxi* sp. n.).

The monophyly of the Mesovelidae is supported by the following characters (Andersen 1982: 78).

- (a) Anterior end of egg obliquely truncate (egg cap developed in most species)
- (b) Eclosion split of egg shell circular, embryonic egg buster absent, eclosion by means of embryonic bladder (for further details see also Cobben 1968)
- (c) Dorsal indentations and apodemes of head absent
- (d) Fore wing venation reduced (wings with only 3 closed cells as compared to the plesiomorphic number of 4–5 closed cells in gerromorphan bugs)
- (e) First abdominal mediotergite of macropterous adult form with a pair of longitudinal ridges
- (f) A specialized ejaculatory bulb and pump present in the male genital tract (see also Cobben 1978).

Female mesovelids have a well developed ovipositor with long and serrate gonapophyses and large gonoplags (Scudder 1959, Andersen 1982). Chiefly because of a superficial resemblance with the ovipositor of other Heteroptera (e.g., Leptopodomorpha and Cimicomorpha), Andersen (1982: 253–256) inferred the female ovipositor of the Mesovelidae to be plesiomorphic, belonging to the ground plan of Gerromorpha. However, the lacinate and serrate ovipositor is functionally associated with the unique egg structure of mesovelids and habit of embedding the eggs in plant tissue instead of placing them superficially on the substrate as inferred to be the plesiomorphic state in gerromorphan bugs (Andersen 1982: 23, 316). As also pointed out by Spence (1984: 46), it is more parsimonious to assume that at least some of the structures of the mesovelid ovipositor must have evolved under selection for improved ability to place eggs within plant tissue. The ovipositor structure should therefore be added to the above list of autapomorphies for the Mesovelidae.

The family Mesovelidae has always been considered quite distinct from other families of semi-aquatic bugs and even removed completely from the infraorder Gerromorpha (previously named Amphibicorisae – Reuter 1912, Scudder 1959). However, all mesovelids share the presence of three

pairs of cephalic trichobothria inserted in cuticular pits, a quadrangular mandibular lever, two pretarsal arolia, and a gynatrial complex including a fecundation canal and tubular spermatheca with other gerrormorphan bugs. Mesoveliids are therefore true cladistic members of the Gerrormorpha (see Andersen 1982 for a detailed discussion) as also implied by contemporary workers (e.g., Cobben 1968, 1978, Štys & Kerzhner 1975, Schuh 1986), and supported by a recent work on the molecular systematics of Heteroptera (Wheeler et al. 1993). According to the hypothesis of phylogenetic relationships between families presented by Andersen (1982: 252–259), the Mesoveliidae is sister-group of the seven other families of Gerrormorpha (Gerridae, Hebridae, Hematobatidae, Hydrometridae, Macroveliidae, Paraphrynoveliidae, and Veliidae).

Andersen & Polhemus (1980: 384–388) discussed the relationships between the genera of Mesoveliidae (not including *Austrovelia* and *Nereivelia*) and presented a phylogenetic tree. This phylogeny was further discussed by Andersen (1982: 77–80), emphasizing its preliminary nature. The difficulties faced in reconstructing the phylogeny of the Mesoveliidae stem, among other things, from the absence of knowledge about the characters of macropterous adult forms in all but a few genera (*Madeovelina*, *Mesovelina*, and *Mesoveloidea*), the obvious modifications of the head (e.g., reduction of eyes) in several species associated with a cryptic life, and the incomplete knowledge for some genera about structure of the internal reproductive organs and eggs.

The results of a reanalysis of the phylogenetic relationships among mesoveliid genera (including those described since 1982) are presented below. The data set (Table 1) was compiled from the above mentioned sources (Andersen & Polhemus 1980, Andersen 1982), from Malipatil & Monteith (1983) and Polhemus & Polhemus (1989).

Characters

The data set (Table 1) comprises 27 characters. These characters and their states are listed below with annotations for most characters (for explanations of terminology of morphological structures, see Andersen 1982).

1. Head extended in front of eyes (0); deflected in front of eyes (1). The head is extended (porrect) in front of eyes in all genera of Mesoveliinae, deflected (declivant) in *Madeovelina* and *Mesoveloidea*. Since the porrect state is shared with other gerrormorphan families (including the family Hebridae), this is probably the plesiomorphic state.

2. Head relatively short, length distinctly less than thorax length (0); prolonged, subequal to or longer than thorax length (1). Among the Mesoveliinae, the head capsule is distinctly prolonged in *Austrovelia*, *Cavaticovelina*, *Cryptovelina*, *Darwinivelina*, and *Phrynovelia*, less so in species of *Mesovelina*, *Nereivelina*, and *Speovelina*. The head capsule is relatively shortest in *Mniovelina* and the two genera of *Madeoveliinae*.

3. Eyes normal in size, globular (0); vestigial (1).

4. Each eye with more than 20 ommatidia (0) with 10–20 ommatidia (1); with only 3–4 ommatidia (2). The mesoveliid eyes are usually large globular and multi-faceted (very large in *Mniovelina kuscheli* Andersen et Polhemus, 1980). A distinct trend towards reduction of the eyes is observed in species which live in caves and other secluded places. *Speovelina mexicanum* Polhemus, 1975, has 30–35 ommatidia; *S. maritima* Esaki, 1929, about 24 ommatidia; *Austrovelina caledonica* (but not *A. queenstandica*; Malipatil & Monteith 1983) and *Darwinivelina fosteri* Andersen et Polhemus, 1980, has about 10 ommatidia; and *Cavaticovelina aaa* (Gagné et Howarth, 1975) has less than 12 small ommatidia in each eye (Gagné & Howarth 1975). The eyes are vestigial in the leaf-litter inhabiting *Cryptovelina* species, each eye composed of 3–4 large ommatidia.

5. Macropterous adult form with ocelli (0); without ocelli (1). The presence of two ocelli at the base of the dorsal head surface undoubtedly belongs to the ground plan of Gerrormorpha (Andersen 1982: 57). Ocelli are found in the macropterous adult form of wing dimorphic *Mesovelina*

species, but absent in *Madeovelia* and *Mesoveloidea* species (which are always macropterous). Unfortunately, this character cannot be scored for other genera of Mesovelinae which are only known in the apterous adult form.

6. Three pairs of cephalic trichobothria forming a regular pattern (0); forming a more or less irregular pattern (1). Mesoveliids have always three pairs of cephalic trichobothria inserted in deep pits on the dorsal head surface (a gerromorphan ground plan character; Andersen 1982: 57). The three pairs of trichobothria are inserted almost equidistantly on each side of the dorsal mid-line of the head in all mesoveliids except *Darwinivelia*, *Madeovelia*, *Mesoveloidea*, *Mniiovelia*, and some *Mesovelia* species.

7. Antenna subflagelliform (0); flagelliform (1). The four-segmented antennae of most Mesoveliidae are of the subflagelliform type, i.e., the two distal segments (together forming the flagellum) are only slightly more slender and longer than any of the two basal segments (scape + pedicel). This type was termed "filamentary" by Andersen & Polhemus (1980: table 1). In the flagelliform type the two distal antennal segments are extremely long, slender, and usually setose. This type is found in *Austrovelia*, *Cryptovelia*, *Mniiovelia*, *Nereivelia*, *Phrynovelia*, and some *Mesovelia* species.

8. Fourth antennal segment uniformly sclerotised throughout (0); with desclerotized zone in middle (1). Zrzavý (1990) presented an excellent analysis of antennal structures in Heteroptera. The gerromorphan antenna is always four-segmented, but the fourth segment of several groups (the family Hebridae in particular, but also *Madeovelia*) has a desclerotized zone in the middle.

9. Antennal segments without spinous hairs (0); with at least a few spinous hairs (1).

10. Ventral head surface not modified (0); with a pair of low, longitudinal ridges (1); with a pair of elevated, longitudinal ridges or carinae (2). The ventral (gular) region of head is relatively long in mesoveliids. Species of *Cryptovelia*, *Mniiovelia*, and *Phrynovelia* have a pair of longitudinal, subparallel ridges between the rostral base and the anterior margin of prosternum which in *Austrovelia*, *Darwinivelia*, and *Nereivelia* are elevated to distinct carinae.

11. Apex of rostrum reaching meso- or metacoxae (0); apex of rostrum distinctly surpassing metacoxae (1).

12. Legs without spinous hairs (0); with weak spinous hairs (1); with strong spinous hairs (2).

13. Prothoracic suture separating tergum and sternopleuron present (0); without such suture (1). The tergal and sternopleural parts of prothorax are usually not delimited by sutures. The presence of such sutures in *Cryptovelia*, *Madeovelia*, and *Mesoveloidea* is here interpreted as plesiomorphic.

14. Mesonotum (apterous form) shorter than or subequal to pronotum in middle (0); longer than pronotum in middle.

15. Posterior margin of metanotum (apterous form) straight (0); sinuate or curved (1). Meso- and metanotum of apterous adult mesoveliids usually forms simple, transverse plates which are shorter than pronotum and have straight intersegmental sutures. Deviations from this state are interpreted as apomorphies.

16. Mesoscutellum (macropterous form) well-developed, triangular (0); reduced, posteriorly rounded (1).

17. Metanotum of macropterous form not modified (0); with a lobate projection in middle (1). As the only gerromorphan bugs, macropterous adults of *Madeovelia* and *Mesoveloidea* have a typical, triangular mesoscutellum. The pseudoscutellum found in macropterous adults of *Mesovelia* are composed by the mesoscutellum and a median lobe on metanotum (Andersen 1982: 68-71).

18. Metathoracic scent reservoir simple, undivided (0); scent reservoir divided (1). The metathoracic scent apparatus of gerromorphan bugs is composed of a pair of lateral scent glands and a scent reservoir which discharge its scent liquid through a scent orifice which opens midventral on metasternum.

Table 1. Taxon-character matrix for the genera of Mesoveliidae. Meaning of characters and their states explained in the text

Character No	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Madeovelia	1	0	0	0	1	1	0	1	0	0	0	1	0	?	?	?	0	?	0	1	0	1	0	1	?	?	?
Mesoveloidea	1	0	0	0	1	1	0	1	0	0	0	1	0	?	?	?	0	0	0	1	1	0	0	0	0	0	0
Cryptovelia	0	1	1	2	?	?	0	1	0	0	1	1	0	0	0	?	?	?	?	?	?	0	0	1	1	0	0
Mniovelia	0	0	0	?	?	1	1	0	0	1	0	0	1	0	1	?	?	?	?	?	?	1	0	1	0	1	1
Darwinivelia	0	1	1	?	?	1	0	0	0	2	0	1	1	0	1	?	?	?	?	?	?	0	0	1	0	0	1
Austrovelia	0	1	0	?	?	0	1	0	0	2	0	0	1	0	1	?	?	?	?	?	?	0	0	?	?	?	?
Phrynovelia	0	1	0	?	?	0	1	0	0	1	0	1	1	0	0	?	?	?	?	?	?	0	0	1	0	1	?
Nereivelia	0	1	0	?	?	0	1	0	0	2	1	0	1	0	0	?	?	?	?	?	?	0	0	?	?	?	?
Speovelia	0	0	0	?	?	0	0	0	1	0	0	2	1	1	1	?	?	?	?	?	?	1	0	?	?	?	?
Cavaticovelia	0	1	1	?	?	0	0	0	1	0	1	1	1	0	0	?	?	?	?	?	?	1	0	1	0	0	1
Mesovelia	0	0	0	0	0	0	0	0	1	0	0	2	1	1	0	1	1	0	1	0	1	0	1	0	0	0	1

num (Andersen 1982: 46–48). In the Mesoveliidae, the scent reservoir is usually a simple subovate sac, but in species of *Cryptovelia*, *Darwinivelia*, *Mniovelia*, and *Phrynovelia*, the sac is at least partially divided into two sacs (Andersen & Polhemus 1980, Andersen 1982: 74–75).

19. Forewing with one closed cell in distal half (0), without a closed cell in distal half (1).

20. Adults dimorphic, macropterous and/or apterous (0); always macropterous (1). The hypothetical ground plan of the Gerrromorpha includes wing dimorphism (adults present in both winged and wingless forms) and a forewing venation composed by three basal, longitudinal veins which merge distally, forming five closed cells (Andersen 1982: 43–46). The winged (macropterous) adult form is only known from species of *Mesovelia*, *Madeovelia*, and *Mesoveloidea*, and species belonging to the two last mentioned genera are probably always winged. The forewing venation of macropterous mesoveliids is reduced, with only three closed cells (Andersen 1982: 73–74). The venation found in *Madeovelia* and *Mesoveloidea* is interpreted as more plesiomorphic than that of *Mesovelia* species (distal part of wing without closed cell).

21. Metatarsal segments increasing in length from first to third segment (0); second tarsal segment as long as or longer than third segment (1).

22. Pretarsi inserted apically on tarsus (0); preapically on tarsus (1). The pretarsal structures (claws, aroha, and parempodia) are primitively inserted on the apex of the last tarsal segment in gerrromorphan bugs. The pretarsus is moved to a preapical or subapical position in members of the large families Gerridae and Veliidae (Andersen 1982: 42). Probably as a result of convergent evolution, a similar state is found in *Madeovelia* and *Mesoveloidea* species (Andersen 1982: 72–73).

23. Ejaculatory bulb of male with slender pump flange (0); with broad pump flange (1). The ejaculatory bulb of the internal genital tract of the male was first recorded from *Mniovelia kuscheli* by Cobben (1968: 172 and fig. 63D) and subsequently found in all mesoveliids examined by Andersen & Polhemus (1980).

24. Ovipositor distinctly serrated (0); with weak, indistinct serration (1).

25. Gonoplaes large (0); small (1). The first gonapophyses are distinctly serrated apically in most mesoveliids. This serration is weakened in *Cryptovelia* and *Madeovelia* species. The gonoplaes are primitively large in mesoveliids but have been reduced in size in *Cryptovelia*, *Mniovelia*, and *Phrynovelia* species.

26. Gynatrial sac small (0); large (1). The gynatrial complex of female gerrromorphans is composed of a gynatrial sac, a fecundation canal, and a long tubular spermatheca (Andersen 1982: 52–53).

The gynatrial sac is relatively small in all mesoveliids except in *Mniovelia kuscheli* (Andersen & Polhemus 1980; Andersen 1982, fig. 94).

27. Anterior end of egg without pseudopercular rim (0); with complete pseudopercular rim (1). The structure of the eggs of several species of Mesoveliidae was described by Cobben (1968), Andersen & Polhemus (1980), and Andersen (1982: 63–64). Typically, a distinct pseudopercular rim surrounds the egg cap on the anterior, truncated end of the egg. This rim is indistinct or absent in *Cryptovelia*, *Mesoveloidea*, *Speovelia*, and some *Mesovelia* species.

Cladistic analysis

The taxon-character matrix (Table 1) was subjected to a cladistic analysis using the parsimony program Hennig86 (Farris 1988). Most characters have only two states. Among the three characters with more than two states, character nos. 10 and 12 were treated as additive (ordered). The result of the cladistic analysis was a single, 50 steps long tree (ci= 60, ri= 65) with the topology depicted in Fig. 11.

The cladogram (Fig. 11) shows the most parsimonious hypothesis of relationships between the genera of Mesoveliidae with the character-states supporting these relationships placed on the branches of the cladogram. The monophyly of the subfamily Madeoveliinae Poisson, comprising the genera *Madeovelia* and *Mesoveloidea*, is supported by several apomorphies of which the shape of the head (1–1), loss of ocelli (5–1), loss of apterous adult form (20–1), and preapical insertion of claws (22–1), are the most reliable. The remaining 9 genera comprise the subfamily

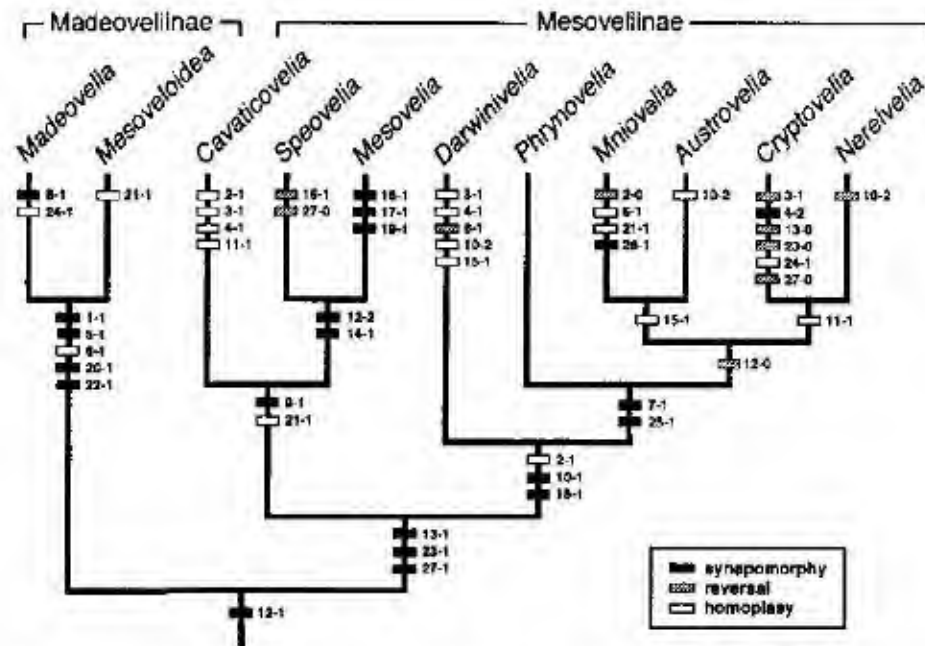


Fig. 11. Cladogram of relationships between the genera of Mesoveliidae. Black cross-bars indicate synapomorphic character changes between nodes, hatched cross-bars indicate synapomorphies that are reversals, open cross-bars indicate homoplasies. Meaning of character numbers and character states explained in the text.

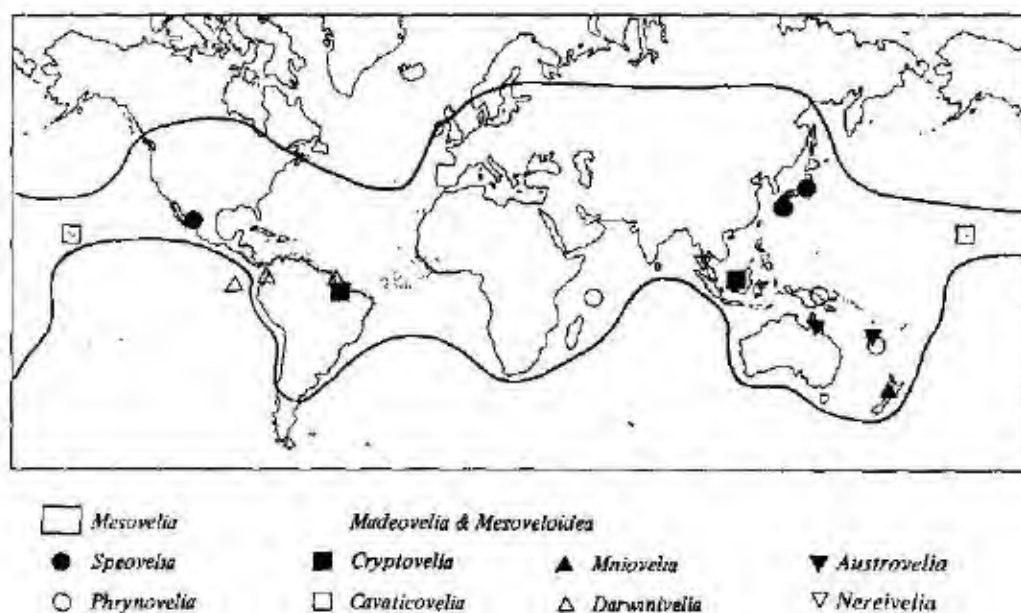


Fig. 12 World map showing the distribution of the genera of Mesoveliidae.

Mesoveliinae, the monophyly of which is supported by the structure of the thorax (13–1), ejaculatory bulb (23–1) and egg (27–1). The group composed by *Cavaticovelia*, *Speovelia*, and *Mesovelia* is only weakly supported whereas the remaining 6 genera probably constitute a monophyletic group supported by the ventral modifications of the head (10–1) and divided scent reservoir (18–1). The group composed by *Phrynovelia*, *Mniovelia*, *Austrovelia*, *Cryptovelia*, and *Nereivelia* is supported by the flagelliform antenna (7–1) and small gonopods (25–1). The cladogram (Fig. 11) suggests sister-group relationships among the four last mentioned genera, but without strong support by characters.

In conclusion, the present cladistic reanalysis of the Mesoveliidae supports the monophyly of the two subfamilies proposed by Andersen (1982), but not the relationships between the genera of Mesoveliinae proposed by Andersen & Polhemus (1980) and Andersen (1982: 98).

ZOOGEOGRAPHY

Andersen & Polhemus (1980) and Andersen (1982: fig. 610) mapped the world distribution of the mesoveliid genera and discussed their biogeographical implications. Spangler (1990) and Andersen (1995a) presented updated check-lists and records of distribution for the species of *Mesovelia* for the New World and Palearctic Region, respectively. The distributions of mesoveliid taxa described since 1980 are here added to the map (Fig. 12). In addition, the map depicts a record of an undescribed species of *Phrynovelia* from the Seychelles (N. M. Andersen & D. A. Polhemus, unpublished).

The family Mesoveliidae is distributed worldwide, but apart from the cosmopolitan genus *Mesovelia*, most genera have more restricted ranges of distribution. However, the record of *Cryptovelia*

stylis sp. n. from Borneo, thousands of kilometers from the location (Brazil) of the first species described in the genus, *C. terrestris*, suggests that our present knowledge of distribution probably is incomplete. Nevertheless, it seems fair to assume that the family have had a wide range of distribution for a very long time. This is supported by the finding of a fossil mesoveliid, *Duncanovelia extensa* Jell et Duncan, 1984 (Jell & Duncan 1984), in the Lower Cretaceous (Aptian) of southeastern Australia.

The distribution of the subfamily Madeovelinae is interesting since the occurrence of the two included genera on both sides of the southern Atlantic Ocean (*Madeovelia* in West Africa, *Mesoveloidea* in Middle and South America) may represent a case of vicariance in response to the formation of the Atlantic Ocean following the breakup of Gondwanaland.

The distribution of *Cavaticovelia* (Hawaii) and *Mniovelia* (New Zealand) may be relict, i. e., where the present distribution only represents a fraction of the past distribution. When described (Andersen & Polhemus 1980), *Darvinivelia* was believed to be endemic to the Galapagos Islands, but two other species have now been recorded from both the Atlantic and Pacific coasts of South America (Carvalho 1984; Polhemus & Manzano 1992). Likewise, Malipatil & Monteith (1983) added two new species of *Phrynovelia* (a genus previously only known from Papua New Guinea) from New Caledonia.

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A review of *Onymocoris* (Heteroptera: Thaumastocoridae), with a new species, and notes on hosts and distributions of other thaumastocorid species

Gerasimos CASSIS¹⁾, Randall T. SCHUH²⁾ & Harry BRAILOVSKY³⁾

¹⁾ Department of Entomology, Australian Museum, Sydney, 2000 Australia

²⁾ Department of Entomology, American Museum of Natural History, New York, 10024 U. S. A.

³⁾ Instituto de Biología, Universidad Nacional Autónoma de México, México D. F., México

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Abstract. *Onymocoris styai* sp. n., is described from south-western Western Australia. The host is recorded as *Dryandra sessilis* (Proteaceae). The genus *Onymocoris* Drake et Slater, 1957 is redescribed and the male genitalia of *O. styai* sp. n. and *O. izzardi* Drake et Slater, 1957 are illustrated and described. Additional host and distributional records are provided for other species in the family. Aspects of the biology of the family are reviewed.

Taxonomy, descriptions, host plants, Heteroptera, Thaumastocoridae, Australia

INTRODUCTION

The Thaumastocoridae are a small family of cimicomorphan true bugs whose relationships, morphology and biology are inadequately understood. Drake & Slater (1957) gave the last systematic review of the family. Thaumastocorids are a largely southern hemisphere taxon, with most of the species found in Australia. Their cryptic habits suggest that much remains to be discovered of this highly autapomorphic group. Previous to this work, the family comprised six genera and 18 species (Cassis & Gross 1995). The works of significance on the Australian fauna are those of Kumar (1964), Rose (1965), Slater (1973) and Hill (1988). Schuh & Štys (1991) reviewed the phylogenetic position of the family, proposing a sister-group relationship with the Miridae + Tingidae. Poinar and Santiago-Blay (1997) described a fossil species from Dominican amber (Upper Eocene), suggesting a close relationship to the extant *Xylastodoris luteolus*, and that the family may have close relationships with the stem group Progonocimicidae. Cassis & Gross (1995) and Schuh & Slater (1995) reviewed much of what is known of the family.

The Thaumastocoridae have long fascinated heteropterists because of their novel morphology, austral distribution, and relative scarcity in collections. In a series of recent field trips in temperate Australia, we have collected numerous thaumastocorids, the efforts resulting in the description of a new species and new information on host plants and distributions. This work includes a redescription of the genus *Onymocoris* and provides new information on the morphology of the family. A review of thaumastocorid host plants and biology, and the distribution of the Australian species are also provided.

This work is dedicated to Pavel Štys, longtime friend and colleague, on the occasion of his 65th birthday. Our contribution is a very modest reflection of the seminal nature of Pavel's contributions to heteropterology, especially to our understanding of the morphology and classification of the primitive infraorders Enicocephalomorpha and Diposocoromorpha. Prof. Štys was a visiting fellow at the Australian Museum in 1993 and has had a lasting interest in the Australian fauna, having

described endemic species of Aenictopecheidae, Miridae, Coreidae and Orsillinae. A new species of *Onymocoris* from Western Australia, associated with a proteaceous plant, is named in his honour.

MATERIALS AND METHODS

Museum abbreviations are as follows: Australian Museum = AM; American Museum of Natural History = AMNH; Instituto de Biología, México = UNAM; and Western Australian Museum = WAM. The distribution maps provided are based on the new records in this work, records in Rose (1965), Drake & Slater (1957) and Cassis & Gross (1995), and additional records from the Australian Museum collection.

Measurements are maximum lengths and given in millimetres. Morphological terminology follows that of Schuh & Slater (1995) and Cassis (1995). The jugs of Drake & Slater (1970) are referred to as the mandibular plates. The homologies and nomenclature of the male genitalia follow Dupuis (1970). The illustrations of the phallus have the phallosome removed and the endosoma is not inflated.

TAXONOMY

Onymocoris Drake et Slater, 1957

(Figs 1–25)

Onymocoris Drake et Slater, 1957: 361 (description); Cassis & Gross 1995: 392 (catalogue).

TYPE SPECIES. *Onymocoris hackeri* Drake et Slater, 1957: 364 (by original designation).

DIAGNOSIS. Distinguished from all other thaumastocorines by the mandibular plates equal to or barely surpassing clypeus, and from all thaumastocorids by the declivent head.

DESCRIPTION. Small, length 1.8–2.5, macropterous, elongate-ovoid (Fig. 1), moderately depressed, abdomen laterally expanded, usually with connexiva clearly visible beyond costal margins of hemelytra. Dorsum strongly punctate (Figs 2, 5), evenly on pronotal disc, scutellum, corium and clavus; punctures with depressed peg-like processes, and most often with setae, inserted within punctures and laterad to peg (Fig. 4). Body sparsely to densely setose (Figs 2, 5 and 8), with flattened, decumbent, pale setae.

Head: broad, transverse, wider than posterior width of pronotum (Fig. 2), moderately declivent; vertex convex medially; lateral margins of frons strongly convergent; clypeus acute, tapered anteriorly, terminating ventrally (Fig. 3); mandibular plates convex (Fig. 2), antero-ventrally convex (Fig. 3), equal to or barely surpassing clypeus (Fig. 2); bucculae large, explanate, arcuate (Fig. 3), reaching posterior margin of head; eyes large, depressed, moderately to strongly pedunculate (Fig. 2), postero-laterally oriented, extending beyond posterior margin of pronotum; antennae inserted ventrally, below eyes, A1 about 1/3rd of interocular distance; labium extending beyond forecoxae, first segment broad, contiguous with bucculae, shorter than bucculae.

Thorax: pronotum trapezoidal (Fig. 2), lateral margins rounded, divergent posteriorly, sinuate to weakly emarginate between callosite region and disc (Fig. 2), calli weakly raised, polished, impunctate, glabrous, weakly depressed between calli; disc flattened to weakly convex, posterior margins rounded, posterior margin rectilinear; mesoscutum not visible; scutellum small, subtriangular, weakly convex; proepisternum convex, larger than proepimeron, mesepimeron subquadrate (Fig. 5), metathoracic spiracle not visible, supracoxal lobe extending ventrally as a process; metepisternum subquadrate (Fig. 5), subventrally impressed, metepisternum scent efferent system absent, without peritreme and evaporative areas evident; hemelytra extending between TIX to apex of abdomen; clavus weakly expanded posteriorly, claval suture strongly depressed; costal margins weakly convex, sometimes weakly expanded beyond claval commissure; coxae small, widely separated, coxae

globose, short; femora short, weakly fusiform, not incrassate, tibiae compressed, weakly and evenly expanded distally; tarsi 2-segmented, inserted on disto-dorsal margin of apex of tibiae, small, first segment minute, tibial appendix present on all legs; pretarsi with minute setiform parempodia, without pulvilli-like structures, claws evenly arcuate, thickened basally.

Male abdomen: moderately to strongly expanded laterally (Fig. 8), with 8th tergite and 8th sternite asymmetrical to accommodate pygophore (Fig. 8, 12), dextral margin extending well beyond sinistral margin (Fig. 11), caudad of left paramere; 8th sternite deeply emarginate (Fig. 11), medially almost contiguous with posterior margin of 7th sternite; pygophore tubular (Fig. 9), sinistrally oriented (Figs 9, 10, 12), antero-sinistral margin with subtriangular process (Figs 19, 22), in resting position inserted below 8th tergite (Fig. 11); genital opening spherical, sinistro-lateral in orientation, entirely closed by flattened, sclerotized 11th tergite (Fig. 10); paramere subtriangular (Figs 20, 24), along posterior margin of genital opening extending to opposite margin of genital opening (Fig. 10); phallus with ventral margin lying along distal margin of pygophore, basal plate of articulatory apparatus stirrup-shaped (Figs 20, 24), basally extending to phallotheca, with an arcuate basal plate bridge, with dorsal connectives and capitate processes greatly reduced; the ductus seminis flexible, smooth, secondary gonopore trough-shaped, sclerotized; phallotheca, box-like, sclerotized, opening laterally; endosoma membranous (Figs 20, 23), inflatable, with V-shaped plate-like process.

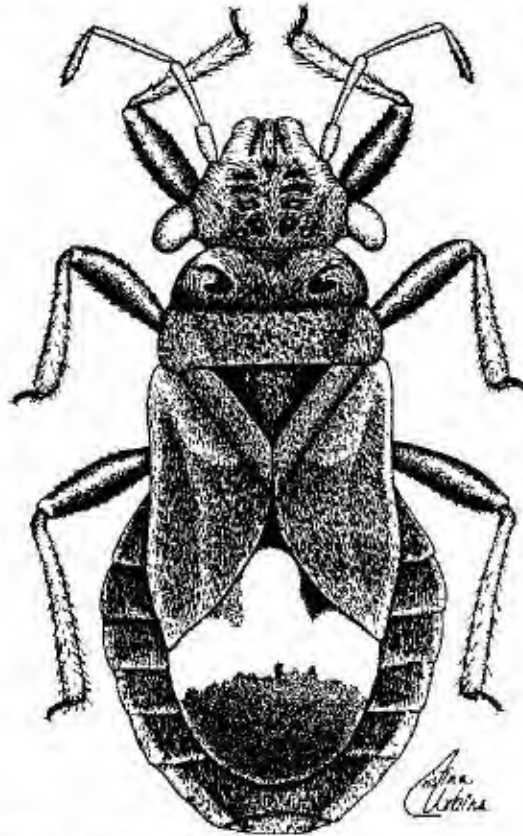


Fig. 1. Habitus of *Orymæcoris styx* n. sp., male.

Female abdomen: symmetrical, ovipositor absent (Fig. 13), with small terminal opening.

DISCUSSION. *Onymocoris* is most clearly differentiated from other thaumastocorines by the length of the mandibular plates, which are subequal in length to the clypeus. This condition is also found in the xylastodorines, and is probably the generalized condition. The head is declivent and the clypeus terminates ventrally, unlike any other thaumastocorid. None of the other characters examined are clear apomorphies for the genus. The restricted host associations with the plant family Proteaceae appear to be diagnostic, although the host of *O. barberi* is unknown. No other group of thaumastocorids has been found on proteaceous plants.

Key to the species of *Onymocoris*
(modified from Drake & Slater 1957)

1. Eyes strongly pedunculate and extending dorsally to level of vertex when viewed from the front of the head; pronotum, scutellum, and posterior one-fourth of corium chocolate brown, and strongly contrasting with pale remainder of hemelytra; hemelytra covering entire abdomen. *O. hackeri* Drake et Slater
- Eyes not so strongly pedunculate and not quite reaching level of vertex when viewed from the front of the head; coloration variable, but pronotum and scutellum never chocolate brown and distinctly contrasting with largely pale hemelytra; connexival area not covered by hemelytra. 2
2. Corial margin strongly sinuate, distinctly expanded beyond apex of claval commissure; pronotal calli convex and protruding, forming sharply angled pronotal margins; pubescence moderately thick, semierect, not silvery in appearance. *O. barberi* Drake et Slater
- Corial margin nearly straight; pronotal calli not prominent, not forming sharply angled pronotal margins; dorsum densely covered with silvery, appressed pubescence. 3
3. Entire exposed portion of dorsum pale, including connexivum, appendages entirely pale, except antennal segment 4 infuscate. *O. izzardi* Drake et Slater
- Head, anterior pronotal lobe, scutellum, connexivum, posterior half of corium, and posterior half of membrane dark, nearly black, contrasting with most of remainder of dorsum; femora mostly dark, tibiae and antennae pale. *O. syisi* sp. n.

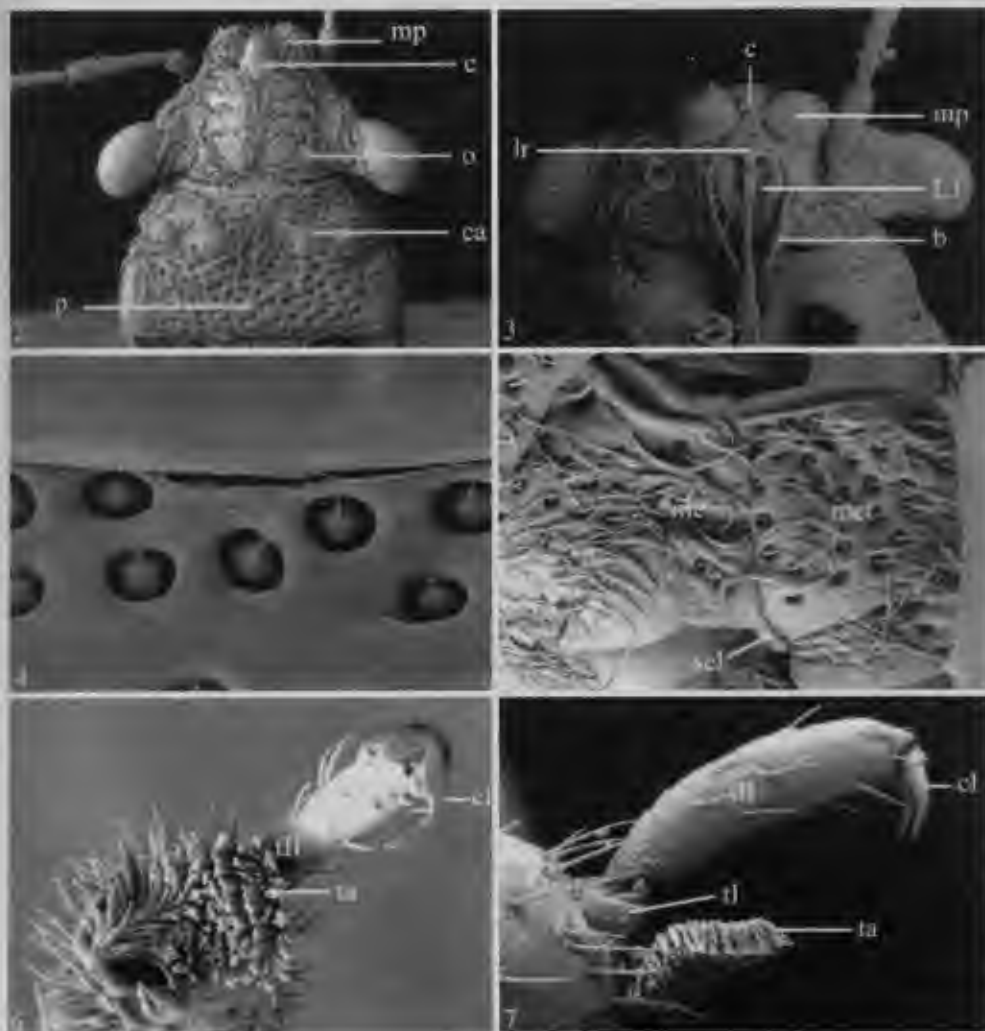
***Onymocoris syisi* sp. n.**
(Figs 1, 2-5, 8-11, 18-21, 25)

TYPE MATERIAL. **Holotype:** Male, AUSTRALIA: Western Australia, Cape Naturaliste National Park, 50 meters, 32° 32' 25" S, 115° 00' 44" E, December 14, 1997, Schuh, Cassis, Brailovsky, ex *Dryandra sessilis* (97-49). Deposited in the Australian Museum, Sydney. **Paratypes:** same data as holotype. Western Australia: Yalgorup National Park, near Martins Tank Campground, 32° 50' 32" S, 115° 39' 44" E, December 14, 1997, Schuh, Cassis and Brailovsky, ex *Dryandra sessilis* (97-46); 30 km S of Armadale 32° 24' 34" S, 116° 16' 51" E, December 18, 1997, Schuh, Cassis and Brailovsky ex *Dryandra sessilis* (97-64). Yalgorup National Park, 32° 50' 09" S, 115° 39' 04" E, November 27, 1998, G. Cassis ex *Dryandra sessilis* [WA98-05]. Pinnacles Desert, Nambung National Park, 30° 36' 16" S, 115° 09' 22" E, November 25, 1998, Cassis, ex *Dryandra sessilis* [WA98-03], Mosman Park, Perth, 32° 01' 33" S, 115° 45' 57" E, 24 November 1998, Cassis, ex *Dryandra sessilis* [WA98-01]. Specimens from each locality are deposited in the AM, AMNH, UNAM and WAM.

DIAGNOSIS. Recognized by the generally darkened head, anterior pronotal lobe, posterior portion of the corium, and particularly, the posterior half of the membrane, the last strongly contrasting with the nearly white anterior half of the membrane. Distinguished from *Onymocoris izzardi*, the only other species presently known from Western Australia, by its much darker coloration, *O. izzardi* being largely cream colored. Distinguished from *O. hackeri* by the more nearly sessile eyes, and coloration, the pronotum, scutellum, and posterior one-third of the corium being castaneous and strongly contrasting with the pale remainder of the corium and membrane in *O. hackeri*. Separated from *O. barberi* by its nearly straight corial margin.

The black coloration of the nymphs contrasts with that found in *O. izzardi*, whose nymphs are entirely yellow.

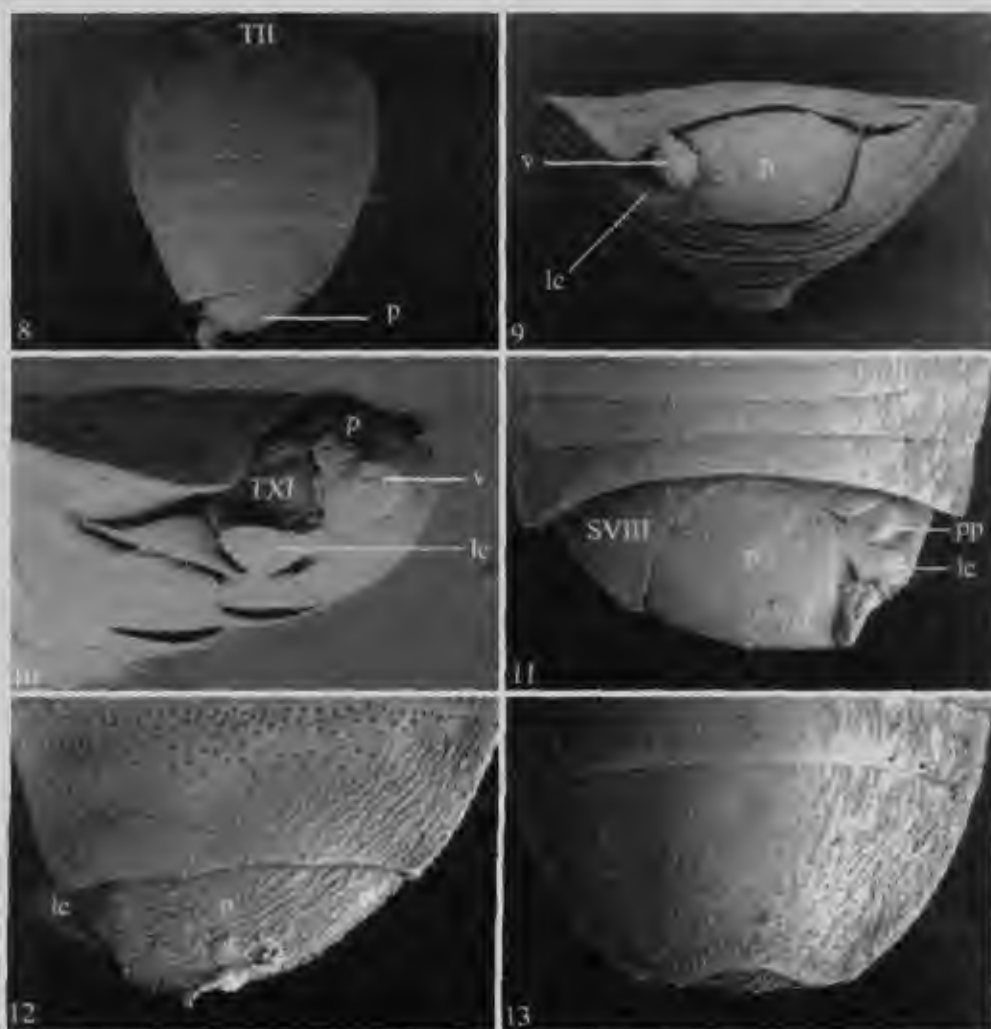
DESCRIPTION. Male. Stout-bodied (Fig. 1). Small, length 1.80–2.12. Submacropterous. Elongate-ovoid, abdomen expanded laterally, maximum width 0.75–0.98, extending well beyond costal margins of hemelytra. Dorsum evenly and densely punctate, with deep, broad punctures, denser elongate, flattened, decumbent, pale setae. Dorsum mostly dark, slate grey, with pronotal disc and anterior 1/3 of hemelytra yellowish brown.



Figs 2–7. *Onymocoris stylus* sp. n. (2–4); 2 – dorsal view of head and thorax, 3 – ventral view of head, 4 – punctation with peg-like structures and setae, 5 – pterothoracic pleura. *Onymocoris izzardi* Drake et Slater (6–7), 6 – male tarsus and tibial process, ventral view, 7 – nymphal tarsus and tibial process, lateral view. Abbreviations: b – bucculae, ca – calli, c – clypeus, cl – claws, lr – labrum, Ll – first labium segment, mp – mandibular plate, me – mesepimeron, met – metepimeron, o – ocellus, p – pronotum, scl – supracoxal lobe, cl – first tarsal segment, tll – second tarsal segment, ta – tibial appendix.

Head: length 0.40–0.44, width 0.64–0.71, interocular distance 0.35–0.43, mandibular plates barely surpassing clypeus; eyes moderately pedunculate (Fig. 2); antennae uniformly stramineous, with short recumbent silvery setae, AI length 0.12–0.14, cylindrical, AII length 0.23–0.26, weakly expanded apically, AIII length 0.23–0.24, subequal in length to AII, AIII length 0.18–0.22, fusiform; labium length 0.53–0.58, extending beyond apices of forecoxae, dark, slate grey.

Thorax: pronotum length 0.33–0.37, posterior width 0.60–0.70, callosite region dark, slate grey; disc stramineous; scutellum; hemelytra extending to TIX of abdomen, corium weakly expanded



Figs 8–13. *Oymocoris styai* sp. n. (8–11): 8 – dorsal view of abdomen, 9 – terminal view of abdomen, 10 – sinistral view of terminalia, 11 – ventral view of terminalia. *Oymocoris eardi* Drake et Slater (12, 13): 12 – dorsal view of terminalia, 13 – ventral view of terminalia. Abbreviations: p – pygophore, TII – second abdominal tergite, SVIII – eighth abdominal sternite, v – vesica.

beyond claval commissure, membrane with anterior 1/2 milky white, remainder brown, sometimes with brown marking adjacent to posterior margin of corium; coxae pale, femora mostly dark, slate grey, with apices stramineous, tibiae stramineous expanded distally, tarsi dark, slate grey, with short recumbent silvery setae.

Abdomen: Figs 8–11; Genitalia: Figs 19–21.

Females. Similar to males in structure, colour, texture and vestiture. Length 1.86–2.04, width 0.94–1.02. Head: length 0.40–0.44, width 0.67–0.76, interocular distance 0.41–0.46; AI 0.12–0.14, AII 0.22–0.26, AIII 0.23–0.25, AIV 0.16–0.22; labium length 0.54–0.63. Thorax: pronotum length 0.35–0.38, width 0.64–0.71.

Nymphs. Entire body castaneous to black; antennae, labium except segment 1 and apex, and tibiae yellow-white; femora and trochanters weakly to strongly infuscate. Entire body clothed with very short, recumbent, scattered, silvery setae. Body very broadly ovoid (Fig. 18), flattened; vertex very broad; eyes not pedunculate; abdominal gland ostioles transverse, slit-like, thickened, at posterior margins of tergites IV and V (Fig. 18, insert).

Discussion. Most of the specimens examined were originally preserved in alcohol. When wet they appear almost entirely black except for the antennae, tibiae, and anterior half of the membrane.



Figs 14–17. *Onymoniscus izardi* Drake et Slater, in copulation; 14 – anterior view, 15 – lateral view, 16 – dorsal view of terminalia, 17 – ventrosinistral view of terminalia. Abbreviations: m – male, f – female, p – pygophore.

When dry, the specimens appear much lighter, in part as a result of the fact that the silvery setae which clothe the body are now visible, whereas on wet specimens they are not.

Host, *Onymocoris styx* sp. n. breeds on *Dryandra sessilis* (Proteaceae).

***Onymocoris izzardi* Drake et Slater, 1957**

(Figs 6, 7, 12, 13, 14–17, 22–24, 25)

Onymocoris izzardi Drake et Slater, 1957: 362; Cassis & Gross 1995: 293

NEW RECORDS. Western Australia: 15 km W of Regan's Ford on Orange Springs Road, 110 meters, 30° 03' 38" S, 115° 34' 31" E, December 09 1997, Schuh, Brailovsky, ex *Banksia grandis* (97–28); Regan's Ford, Moore River, Brand Highway, 110 meters, 30° 58' 47" S, 115° 42' 05" E, December 09 1997, Schuh, Brailovsky, ex *Banksia grandis* (97–29); 48 km N of Regan's Ford on Brand Highway, 110 meters, 30° 36' 58" S, 115° 27' 59" E, December 09 1997, Schuh, Brailovsky, ex *Banksia grandis* (97–30); 11.7 km W of Eneabba, 30 meters, 29° 51' 52" S, 115° 08' 54" E, December 11 1997, Schuh, Brailovsky, ex *Banksia grandis* (97–35); 1.2 km W of Eneabba, 30 meters, 29° 49' 59" S, 115° 14' 43" E, December 11 1997, Schuh, Brailovsky, ex *Banksia grandis* (97–36). Specimens from each locality are deposited in the AM, AMNH and USNM.

DISCUSSION. The nymphs of *Onymocoris izzardi* are entirely yellowish in coloration, with the exception of the red eyes and infusate tarsi.

HOST. We have numerous records of *Banksia grandis* as the host of *Onymocoris izzardi* in Western Australia from the region between Perth and Geraldton. The mating position of this species (Figs 14–17) is discussed below.

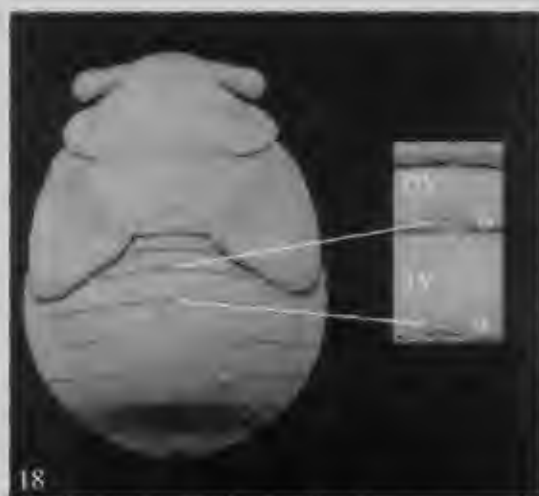


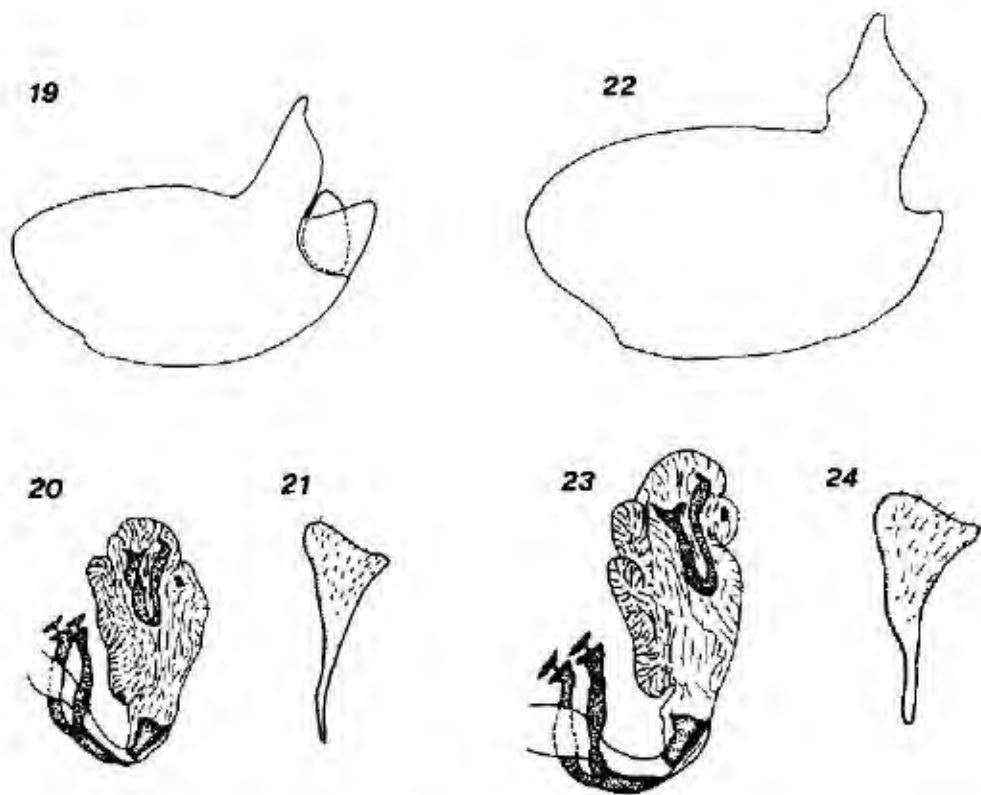
Fig. 18. *Onymocoris styx* sp. n., fifth instar, insert: abdominal glands. Abbreviations: α – ostiole of abdominal glands, TIV – fourth abdominal tergite, TV – fifth abdominal tergite.

***Baclozygum depressum* Bergroth, 1909**

Baclozygum depressum Bergroth, 1909: 333, Drake & Slater 1957: 364, Rose 1965: 144, Slater 1973: 155, Hill 1988: 37, Cassis & Gross 1995: 392

NEW RECORDS. Queensland 9.6 km W of Mitchell, 430 meters, 26° 29' 31" S, 147° 52' 22" E, October 31 1998, Schuh, Cassis, Silveira, ex *Eucalyptus populnea populnea* [CA98-05]. New South Wales 20 km E of Retreat (W. of Uralla), 1000 m, 30° 38' S, 151° 15' E, October 23 1995, Schuh and Cassis, *Eucalyptus* sp. (95-12); Western Australia Conspicuous Beach, Walpole-Nornalup National Park, 10 km E of Nornalup, 30 meter, 35° 02' 14" S, 116° 50' 39" E, December 17 1997, Schuh, Cassis, Bratkovsky, ex *Agonis flexuosa* (97-58), Mosman Park, Perth, 32° 01' 33" S, 115° 45' 57" E, 24 November 1998, Cassis, ex *Agonis flexuosa* [WA98-01]. Specimens from each locality are deposited in the AM and AMNH.

DISCUSSION. Hill (1988) questioned the existence of *Baclozygum depressum* in Western Australia. Nonetheless, the material we list from Conspicuous Beach near Nornalup appears unquestionably to represent *B. depressum* as defined by Hill.



Figs 19-24. *Onymocoris stysi* sp. n. (19-21); 19 – ventral view of pygophore, 20 – phallus, 21 – left paramere. *Onymocoris izzardi* Drake et Slater (22-24); 22 – ventral view of pygophore (tergite XI and left paramere removed), 23 – phallus, 24 – left paramere.

Host We record this species from *Eucalyptus* and grape myrtle, *Agonis flexuosa* (Myrtaceae), the latter being a new host record. This species was previously known from *Eucalyptus* species (Rose 1965, Hill 1988).

***Baclozygum brachypterum* Slater, 1973**

Baclozygum brachypterum Slater, 1973: 151, Cassis & Gross 1995: 392

NEW RECORDS **New South Wales** 72 km N Coonabarabran, 1 km N Big Flat Gully, 250 m, 30° 40' S, 149° 30' E, October 25 1995. Schuh and Cassis, ex *Xanthorrhoea johnsonii* (95-21), **VICTORIA**, Little Desert Nat. Pk., 5-6 km W of McDonald Highway, 150 m, 36° 37' S, 141° 10' E, November 03 1995, Schuh and Cassis, ex *Xanthorrhoea australis* (95-50), 14 km S Nhill, Little Desert Nat. Pk., 150 m, 36° 27' S, 141° 39' E, November 05 1995, Schuh and Cassis, ex *Xanthorrhoea minor lutea* (95-55), 15 km S of Cann River, 250 m, 37° 12' S, 149° 08' E, November 08 1995, Schuh and Cassis, ex *Xanthorrhoea resinifera* (95-59), **South Australia** 14.5 km NW of Keith, 100 m, 36° 00' S, 140° 16' E, November 03, 1995, Schuh and Cassis, ex *Xanthorrhoea semiplana semiplana* (95-48), 21.8 km S of Bews, Ngarkat Conservation Park, 90 meters, 35° 35' 49" S, 140° 27' 41" E, November 09 1998, Schuh, Cassis, Silveira, ex *Xanthorrhoea semiplana semiplana* [CA98-37], 38.1 km S of Bews, Ngarkat Conservation Park, 90 meters, 35° 39' 35" S, 140° 26' 56" E, November 09, 1998, Schuh, Cassis, Silveira, ex *Xanthorrhoea semiplana semiplana* [CA98-38], Mosman Park, Perth, 32° 01' 33" S, 115° 45' 57" E, 24 November 1998, Cassis, ex *Agonis flexuosa* [WA98-01]. Specimens from each locality are deposited in the AM and AMNH.

DISCUSSION Slater (1973) described *Baclozygum brachypterum* from the Perth region of Western Australia. As the name indicates, this species was based on brachypterous specimens. Most specimens that we have collected have the hemelytra greatly abbreviated, covering only the first abdominal tergum. However, we have collected macropterous females from Ngarkat Conservation Park, South Australia and Mosman Park, Western Australia, which are the first records of wing polymorphism for this species. This species is easily recognised by the sexual dimorphism in abdominal coloration, and in most specimens the hemelytra are uniquely shortened. Our fieldwork has produced specimens from several localities in south-eastern Australia, dramatically increasing the known range, and suggesting that this species may have a trans-continental distribution. There appears to be no doubt that the specimens represent one species, and comparison with Slater's material indicates that despite some variability, particularly in the shape and denticles on the mesial margin of the mandibular plates, the total range of variation is found in both eastern and western populations.

Host Slater (1973) based his description on specimens collected by sweeping in areas dominated by native vegetation, but he was unable to identify a specific host. We have now established that this species is found in association with *Xanthorrhoea preissii* in south-western Australia. Our fieldwork in eastern Australia indicates that *Baclozygum brachypterum* feeds on five other identified species of *Xanthorrhoea* (Table 1).

***Thaumastocoris australicus* Kirkaldy, 1908**

Thaumastocoris australicus Kirkaldy, 1908: 778, Drake & Slater 1957: 366, Slater 1973: 155, Cassis & Gross 1995: 393

NEW RECORDS **Queensland** 11 km E of Adavale, 300 meters, 25° 57' 16" S, 144° 41' 05" E, November 02, 1998. Schuh, Cassis, Silveira, ex *Eucalyptus populnea populnea* [CA98-13], 9 km WSW of Adavale, 270 meters, 25° 54' 39" S, 144° 30' 51" E, November 02, 1998, Schuh, Cassis, Silveira, ex *Eucalyptus populnea populnea* [CA98-14], 45 km N of Quilpie, 280 meters, 26° 20' 32" S, 144° 18' 28" E, November 02 1998. Schuh, Cassis, Silveira, ex *Eucalyptus* sp. [CA98-16], **South Australia** Scorpion Springs Conservation Park, 120 meters 35° 29' 14" S, 140° 51' 58" E, November 10 1998. Schuh, Cassis, Silveira, ex *Eucalyptus costata* [CA98-42], 5 km N Yunta toward Arkaroola, 250 m, 132° 32' S, 139° 33' E, October 29, 1995, Schuh and Cassis, ex *Eucalyptus* sp. (95-

35); 51 km NW of Morgan, 150 m, 33° 35' S, 140° 00' E, November 01, 1995, Schuh, Cassis, and Gross, ex *Eucalyptus socialis* (95-44) (AM and AMNH); Bogan River, J. Armstrong (AM). Specimens collected by Schuh and Cassis are deposited in the AM and AMNH.

DISCUSSION. Specimens identified as *Thaumastocoris australicus* possibly represent more than one species, and may be confused with the closely related species, *T. hackeri* and *T. macqueeni*. We have collected additional specimens from New South Wales, Victoria and Western Australia that fit within this complex, but these could not be positively identified without considerable more study and have been excluded from present considerations.

HOST. This species was previously known to feed on species of *Acacia* (Kumar 1964, Slater 1973). Our field work extends the host associations of *Thaumastocoris australicus* to *Eucalyptus* species from Queensland and South Australia.

Thaumastocoris hackeri Drake et Slater, 1957

Thaumastocoris hackeri Drake et Slater, 1957: 367; Rose 1965: 141; Slater 1973: 155; Hill 1988: 37; Cassis & Gross 1995: 393.

NEW RECORDS. New South Wales: approx. 3 km N Lansdowne via Taree, 30° 8' S, 145° 30' E, November 2, 1990, G. and T. Williams, ex *Schizomeria ovata* (AM); Horton's Creek, near Cloud's Creek, 30° 05' S, 152° 63' E, August 28, 1961, C.N. & A.S. Smithers (AM).

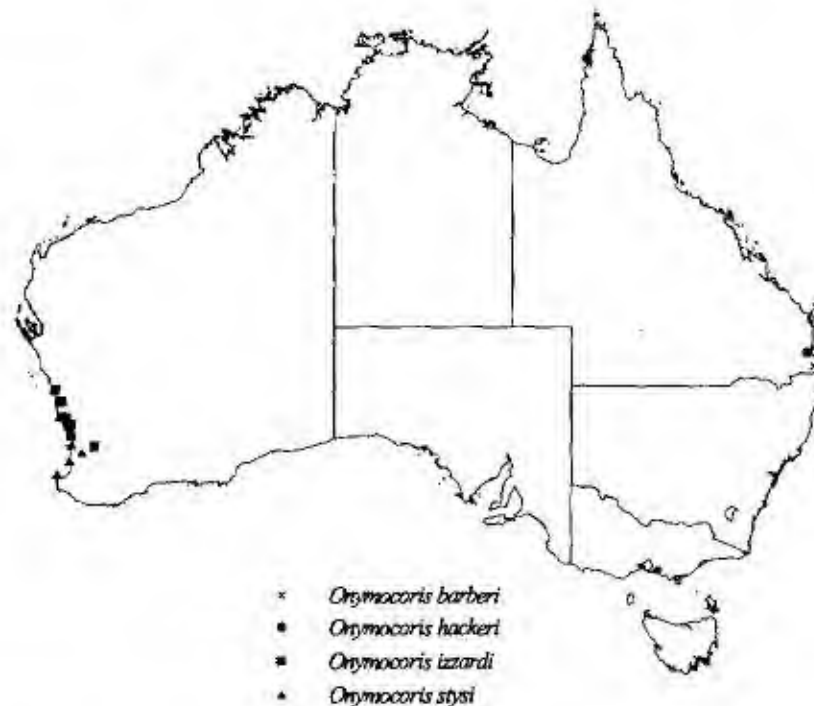


Fig. 25. Distribution of *Onymacoris* Drake et Slater species.

Host. The new record of this species from near Taree is of interest because it was captured in a pollination study, in association with the flowers of a species of the plant family Cunoniaceae (Williams pers. comm.).

***Thaumastocoris petilus* Drake et Slater, 1957**

Thaumastocoris petilus Drake et Slater, 1957: 367; Slater 1973: 154; Cassis & Gross 1995: 394.

NEW RECORDS. **Western Australia:** Brand Highway, 8.2 km N of Encabba, 29° 44' 46" S, 115° 15' 14" E, October 31, 1996, Schuh and Cassis (96-46), ex *Melaleuca raphiophylla*; Mosman Park, Perth, 32° 01' 33" S, 115° 45' 57" E, November 29 and December 05, 1998 G Cassis ex *Melaleuca* sp. [WA98-08, 22]. **South Australia:** 18 km S of Brews, Ngarkat Conservation Park, 60 meters, 35° 33' 07" S, 140° 25' 59" E, November 09, 1998 Schuh, Cassis, Silveira, ex *Melaleuca* sp. [CA98-36]. Specimens from each locality are deposited in the AM and AMNH.

DISCUSSION. The new distribution records from Western Australia and South Australia indicate that this species is probably widespread across Australia in drier habitats. The species was first described from Victoria and the specimens from the Western Australian localities represent a significant geographic disjunction. These specimens however exhibit enough variation from the original description, that a comparison with type specimens is required to be certain of the conspecificity of all the known specimens.

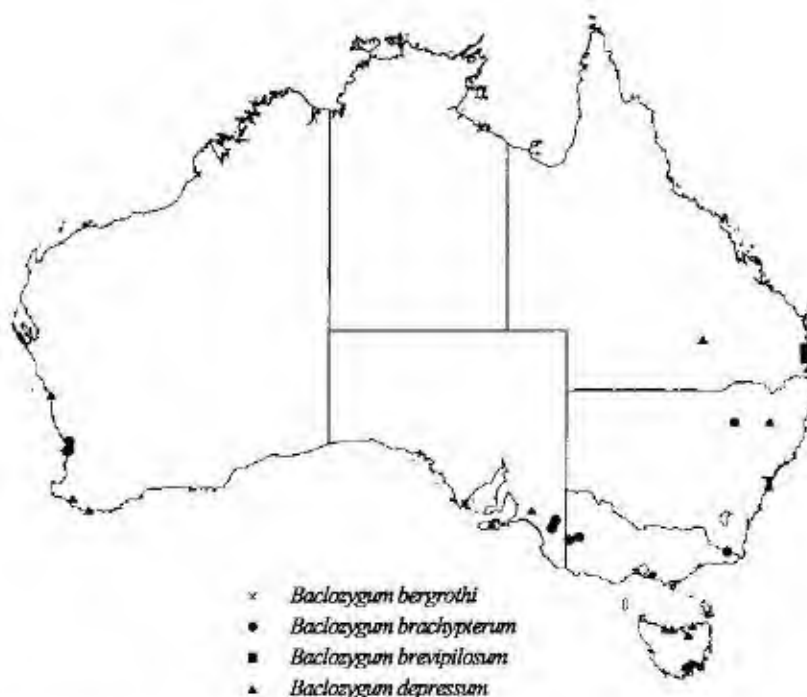


Fig. 26. Distribution of *Baclozygum* Bergroth species.

Host. Our collections confirm Slater's (1973) host record, *Melaleuca raphiophylla* (Myrtaceae). The species has also been collected from undetermined species of *Melaleuca* from Western Australia and South Australia.

MORPHOLOGY

The male abdomen and terminalia of the Thaumastocoridae are distinctive, exhibiting pre-genital asymmetry that is unknown in any other cimicomorphan, and of a type analogous to some Diposcoromorpha and Nepomorpha. In all thaumastocorids the eighth abdominal segment is strongly modified, with the sternite grossly asymmetrical. The condition of the pygophore is autapomorphic, and is strongly oriented to the left or right side. The orientation of the pygophore can vary within a genus, and even within the species *Xylastodoris luteolus*. The genital opening is spherical and when the phallus is in repose, the opening is entirely covered by a spherical, sclerotized plate, that is tentatively interpreted as the eleventh tergite.

The male genitalia of the two species of *Onymacoris* investigated in this work are very similar in structure, although, the male genitalia in *O. stysi* sp. n. are considerably smaller than in *O. izzardi*. The genitalia of these species are very similar to those of *Baclozygum depressum* and *Thaumastocoris australicus* (Drake & Slater 1957, Kumar 1964). This possibly indicates that within the Thau-

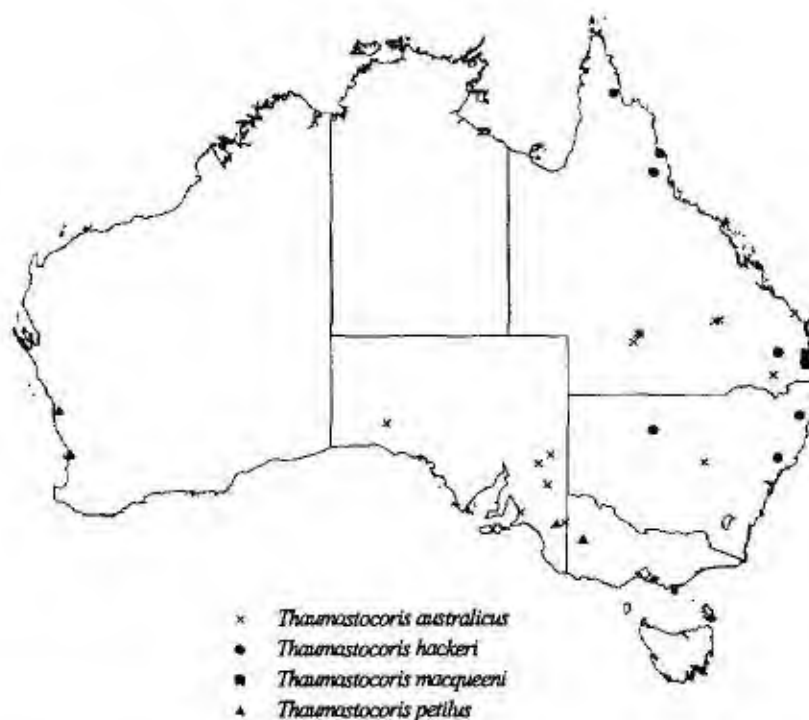


Fig. 27. Distribution of *Thaumastocoris* Kirkaldy species.

mastocorinae, there is little variation of the phallus and that it will not afford significant taxonomic or phylogenetic value.

The phallus is divided into the articulatory apparatus, phallosome and endosoma. We support Drake and Slater's (1957) contention that the endosoma is not further subdivided into conjunctiva and vesica. No distal sclerotized process was observed and any extension of the ductus seminis beyond the secondary gonopore was unclear. We interpret the trough-like sclerotization at the base of the endosoma as the secondary gonopore, which bounds the apex of the ductus seminis. The male phallus appears to be typical of Cimicomorpha, and is reminiscent of Tingidae and some Miridae. Character states of the phallus that may be diagnostic for the Thaumastocorinae possibly include: the arms of the articulatory apparatus in Thaumastocorinae very narrow (with basal foramen large), the flexible, smooth ductus seminis, the trough-like secondary gonopore, the box-like phallosome, and the distal V-shaped sclerotization of the endosoma.

BIOLOGY

Host Plant Associations

Life histories of the Thaumastocoridae are poorly understood with most information derived from Baranowski (1958) for the New World species *Xylastodoris luteolus* and Hill (1988) for Australian thaumastocorine species. All available evidence suggests that the family is exclusively phytophagous, and the species are associated with either the infructescences, inflorescences or leaves of trees and shrubs. Hosts have now been recorded for 16 of the 19 described species (Table 1). Unlike the Xylastodorinae, where most species are recorded presently as host plant specific (Couturier et al. 1998), many of the thaumastocorine species are known from more than one plant species. Only *Onymocoris* species, *Baclozygum brevipilosum* and *Thaumastocoris peilus* are known from a single host.

Patterns of host association can be recognised, even though thaumastocorids are known from six plant families. The most curious association of thaumastocorids is with two unrelated families of monocots. All Xylastodorinae species are known from palms, although the species have been taken from eight palm genera, with *Discocoris drakei* known from three palm genera (Couturier 1998). *Baclozygum brachypterum* is recorded here from the Xanthorrhoeaceae, with the association evidently at the generic level, as this species has been taken from six species of *Xanthorrhoea*. This species is commonly encountered in eastern Australia, particularly in semi-arid areas of the Murray-Darling basin (Fig. 26). Slater (1973) originally described *Baclozygum brachypterum* from Western Australia although he recorded no host information. We found this species in association with *Xanthorrhoea preissii* in a disturbed habitat, in a park in suburban Perth. We spent considerable time searching for this thaumastocorid species on *Xanthorrhoea*, and the related genera *Dasypogon* and *Kingia*, in other parts of Western Australia, without success. This represents the first association of Heteroptera with the Xanthorrhoeaceae, although at one particular location (Yalgoo National Park, Western Australia), anthocorid nymphs were encountered in the same microhabitat. In general, there are few records of the Heteroptera exploiting monocots in Australia. Aside from the typical association of family-groups such as the Blissidae and Stenodemini (Miridae), and genera such as *Ontiscus* Stål, 1874 and *Pachygrontha* Germar, 1837 (Lygaeidae sensu lato), most phytophagous Australian Heteroptera appear to be found on dicots. However, this new monocot association suggests continued examination of these angiosperms may be productive. For example, we have found the orthotyline genera *Kirkaldyella* Poppius, 1921 and *Woodwardiella* Carvalho, 1973 consistently associated with the monocot genus *Lomandra* (Lomandraceae). The discovery of monocot feeding in both the Xylastodorinae and Thaumastocorinae is suggestive that such habits may be generalised for the family. However, there can be no suggestion that this has co-

Tab 1 Host plant species and families, and microhabitats of Thaumastocoridae

Thaumastocoridae species	Host plant species	Host plant family	Microhabitat	Reference
<i>Disocoris drakei</i>	<i>Phylephas</i> sp. <i>Jessenia batana</i> <i>Oenocarpus mapora</i> <i>Mauritia flexuosa</i> <i>Socratea montana</i> <i>Bulia yatai</i> <i>Euterpe edulis</i> <i>Roystonea regia</i>	Palmae Palmae Palmae Palmae Palmae Palmae Palmae	inflorescences inflorescences inflorescences inflorescences inflorescences young leaves, pinnae and inflorescences	Schuh (1975) Couturier et al (1998) Couturier et al (1998) Couturier et al (1998) Slater & Schuh (1996) Viana & Carpintero (1981) Kormilev (1955) Baranowski (1958)
<i>Baclozygum bergrothi</i> <i>Baclozygum brachypetrum</i>	unknown <i>Xanthorrhoea australis</i> <i>X. johnsonii</i> <i>X. minor lutea</i> <i>X. reinferu</i> <i>X. semiplana semiplana</i> <i>X. preussi</i>	Xanthorrhoeaceae	leaf axils leaf axils leaf axils leaf axils leaf axils leaves	this work this work this work this work this work Rose (1965) Hill (1988)
<i>Baclozygum brevipilosum</i> <i>Baclozygum depressum</i>	<i>Eucalyptus trachyphloia</i> <i>Eucalyptus globulus</i> <i>E. populnea populnea</i> <i>E. pulchella</i> <i>E. trachyphloia</i> <i>E. viminalis</i> <i>Agonis flexuosa</i> unknown <i>Banksia integrifolia</i>	Myrtaceae Myrtaceae	leaves leaves leaves leaves leaves leaves leaves, flowers	Rose (1965) Hill (1988) this work Hill (1988) Rose (1965) Hill (1988) this work
<i>Ozymocoris barberi</i> <i>Ozymocoris hackeri</i>	unknown <i>Banksia grandis</i> <i>Dryandra sessilis</i> <i>Acacia Cunninghamhami</i> <i>Acacia maidenii</i> <i>Eucalyptus costata</i> <i>E. socialis</i> <i>E. populnea populnea</i> <i>Elaeocarpus obovatus</i> <i>Schlotheimia ovata</i>	Proteaceae Proteaceae Mimosaceae Mimosaceae Myrtaceae	leaves leaves leaves leaves leaves leaves leaves leaves flowers	Drake & Slater (1957) Rose (1965) this work this work Kumar (1964) Slater (1973) this work this work this work Rose (1965) this work
<i>Thaumastocoris hackeri</i>	unknown <i>Melaleuca thaphiophylla</i> unknown	Elaeocarpaceae Cunoniaceae	leaves leaves	Slater (1973)
<i>Thaumastocoris macqueeni</i> <i>Thaumastocoris psittacus</i> <i>Wehrhahn chinai</i>	unknown	Myrtaceae	leaves	Slater (1973)

evolutionary significance, as the Xanthorrhoeaceae and Palmae are placed in unrelated clades within the monocots (Rudall 1995).

The other species of *Baclozygum* Bergroth, 1909 with recorded hosts have been taken from trees belonging to the Myrtaceae. *Baclozygum brevipilosum* has been found on *Eucalyptus trachyphloia* in south-eastern Queensland. *Baclozygum depressum*, a widespread temperate species, has been taken from five species of *Eucalyptus*, although Hill (1988) doubted that the specimens identified by Rose (1965) from *E. trachyphloia*, are *Baclozygum depressum*. We also found *B. depressum* on grape myrtle, *Agonis flexuosa* (Myrtaceae) in coastal areas of south-western Western Australia. The divergent host associations of *Baclozygum brachypterum* (on *Xanthorrhoea* species) and the myrtaceous inhabiting *Baclozygum* species is suggestive of an alternative taxonomic arrangement between these taxa.

Previous to this work the only known host association of *Onymocoris* species was *O. hackeri* from *Banksia integrifolia*. We record here two new host associations, *Onymocoris izzardi* from *Banksia grandis* and *Onymocoris styli* sp. n. from *Dryandra sessilis*. This suggests that *Onymocoris* is restricted to species in the plant family Proteaceae, and possibly in the *Banksia-Dryandra* complex of genera. Both of these genera show significant radiations in Western Australia, with 60 of the 75 known species of *Banksia*, and all of the 95 described species of *Dryandra*, occurring in south-western Western Australia. For this reason it would be reasonable to expect that any additional new species of *Onymocoris* are likely to be found in Western Australia.

The genus *Thaumastocoris* Kirkaldy, 1908 has the broadest host associations, and is known from four plant families. *T. australicus* is known from two species of *Acacia* and three species of *Eucalyptus*. These plant genera are commonly associated, and host switching between them is not out of the question. There may be a species complex, presently attributed to *Thaumastocoris australicus*, and workers need to separate populations by host, as they may represent separate species. *T. hackeri* has the most curious host associations, known presently from two species, in the families Elaeocarpaceae and Cunoniaceae, from which there are no other thaumastocorid records. *Thaumastocoris petilus* is known from *Melaleuca raphiophylla*, the host association being reported by Slater (1973) from Western Australia. We established the same host for this species from another Western Australia locality.

Of the nine Australian species of thaumastocorids with recorded host plants, three species and two genera are known from *Eucalyptus* species. The association of the Heteroptera with this dominant Australian plant genus is not common. Aside from tight associations of particular pentatomorphan genera such as *Amorbus* Dallas (Coreidae) and *Poecilometis* Dallas, 1851 (Pentatomidae), few true bugs have penetrated the plant defences of *Eucalyptus*, in the way that many sternorrhynchous and auchenorrhynchous Hemiptera have. We have recently discovered that certain mirid species in the Saturniimirini and Phylini are associated with new meristematic tissues in *Eucalyptus* species, although no general supraspecific pattern has been found. There is a need for heteropterists to focus some attention to collecting on *Eucalyptus* as it may yield either new thaumastocorid species or new specific host associations.

Mating

The coupling position of *Onymocoris izzardi*, described here, is the first record of mating habits in the Thaumastocoridae. The position is defined as male dominant and unidirectional in orientation (Figs 15-17). It is assumed that the illustrated pair was in final mating position because several alcohol-preserved pairs were found in the same position. The male clasps the lateral margins of the female abdomen with the ventro-subapical aspects of the tibiae. The abdomen is weakly ventroflexed (Fig. 15) and the pygophore is further ventroflexed (Figs 16, 17), at about a 30° angle to the long axis of the abdomen. The pygophore has a process above the genital opening, which locks

under the eighth abdominal sternite. Once the lock is released the entire pygophore is free, aside from the basal articulation, and is engaged in copulation. The apices of the pygophore and paramere insert in the female medio-caudally (Fig. 17), whereupon the phallus presumably engages with the internal female genitalia, and the endosoma inflates. The paramere (Fig. 17) appears to remain in its original position and possibly acts as a guide to the phallus.

DISTRIBUTION

Thaumastocorids are widely distributed in Australia. The majority of species have been collected in the coastal areas of eastern Australia and south-western Australia, with six species known from Queensland, five from Western Australia and four from New South Wales. However, our collecting reveals that many species are also found in the interior of Australia, and five of the thaumastocorid species are very broadly distributed and are known from at least two states. For example, *Baclozygum bracypterum* and *B. depressum* have trans-continental distributions (Fig. 26). *Thaumastocoris australicus* is known from the semi-arid areas of Queensland, NSW and South Australia (Fig. 27), and there is some evidence that it may also occur in south-western Australia.

The genus *Onymocoris* comprises four species, which have largely non-overlapping distributions (Fig. 25). Two species, *O. styxi* sp. n. and *O. izzardi*, exist in the temperate zone of south-western Australia, in coastal heathlands that are dominated by proteaceous plants. The other two species, *O. barberi* and *O. hackeri*, are known from a total of three locations in Queensland, and it is premature to reach any conclusions about their distribution.

The distribution of *Baclozygum* is primarily temperate, with three of the four known species, being found south of Brisbane. One specimen of *B. depressum* has been collected from Cape York, which suggests that the species may be ubiquitous. *Thaumastocoris* has the most widespread distribution (Fig. 27), and most species have broadly overlapping distributions.

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Larval and adult dorso-abdominal scent glands and androconia of central European Pentatomoidea (Heteroptera)

Jitka DAVIDOVÁ-VILÍMOVÁ¹⁾ & Miloš PODOUBSKÝ²⁾

¹⁾ Department of Zoology, Charles University, Viničná 7, CZ-128 44 Praha 2, Czech Republic

²⁾ Erbenova 17, CZ-446 02 Jablonec nad Nisou, Czech Republic

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Abstract. The dorso-abdominal scent glands of larvae (26 species from 23 genera) and adults (43 species from 34 genera) of central European Pentatomoidea are described and illustrated. At least one gland is structurally persistent, and probably functional, in adults of almost all the species studied. The existence of a morphological sexual dimorphism was either confirmed, or newly established, in some representatives of the families Plataspidae, Cydnidae, and Pentatomidae, particularly in the subfamily Asopinae. The data about the larval glands are new for 17 species, those about the adult glands for seven species, and those about both the stages for five species. The androconia were described in both sexes of *Odontocoris fuliginosa* (Linnaeus, 1761) (Scutelleridae), providing the first record in a scutellerid female. The persistence of the dorso-abdominal scent glands in adults, with the anterior gland functional, is a common feature in Pentatomoidea. The larval versus the adult gland patterns; correspondence of the number of ductules with the structural state of glands; variation of the gland patterns within Pentatomoidea, and existence of a sexual dimorphism are aspects discussed.

Morphology, ontogeny, function, dorso-abdominal scent glands, androconia, sexual dimorphism, Pentatomoidea

INTRODUCTION

The development of the larval dorso-abdominal and the adult metapleural scent glands is considered an autapomorphy of the taxon Heteroptera within Insecta. The complete reduction of the dorso-abdominal glands and their functional substitution by the metapleural glands in adults was assumed by many former authors (e. g., China 1955, Gupta 1961). A high number of the dorso-abdominal glands is considered the plesiomorphy, reduced number the apomorphy (e. g., Štys 1959, Gupta 1964). Cobben (1978) reviewed published opinions on phylogeny of the scent glands. Formerly, the unpaired glands were regarded as the plesiomorphic state of character. However, the opinion of Polivanova (1960), that the paired gland arrangement represents the plesiomorphic state in Pentatomoidea, has been mostly accepted. This author proved the origin of glands as six paired structures in pentatomoid embryos. The reduction of the gland number and/or their fusion into an unpaired structure, spreading from the posterior to the anterior segments, are considered to be apomorphies.

Persistence in adults

Not only the persistence, but even the functionality of the dorso-abdominal glands in adults from various heteropteran taxa, has been recognized by many authors in the last few decades. Verhoeff (1893) was the first, who mentioned the persistence of the dorso-abdominal glands in heteropteran adults, and reported three pairs of the gland ostioles in Pentatomoidea (referred as Pentatomidae). Boselli (1932), Henrici (1939), Dupuis (1947, 1949), Staddon (1979), and Aldrich et al. (1995) and

others ascertained the persistence of pentatomoidean adult dorso-abdominal glands. Aldrich (1988a, 1988b, 1991, 1995, 1996) and Staddon (in press) summarized the comprehensive data about the persistence of the adult dorso-abdominal glands in Heteroptera and particularly Pentatomoidea. Other studies, concerning more species, were published recently, e. g., Evans et al. (1990), Staddon (1990) – Acanthosomatidae; Farshbaf et al. (1994) – Pentatomidae.

While Dupuis (1947) did not consider the persistence of the adult dorso-abdominal glands as usual, Staddon et al. (1987) suggested to include a retention of activity of the adult anterior dorso-abdominal gland into the scent gland characteristics of the pentatomoid families. The persistent adult dorso-abdominal scent glands were found in various representatives of Pentatomoidea, including many scutellerids, in spite of the hypertrophic scutellum covering their whole abdomen. Kaufmann (1966) described and illustrated the obvious paired anterior, and the small unpaired median and posterior glands in *Callidea dregii* (Germar, 1832). Hamilton et al. (1985), Gough et al. (1986), and Staddon et al. (1987) described persistent adult glands in other species, *Hotea gambiae* (Westwood, 1837), *Sphaerocoris annulus* (Fabricius, 1775), and *Tectocoris diophthalmus* Stål, 1870. The gland morphology together with the composition of secret was described except of secretion emission from the glands completely covered by the scutellum.

Functional median and/or posterior glands, and often the anterior gland, were recognized and evidenced in several other heteropteran families; Reduviidae (e. g., Carayon et al. 1958, Aldrich 1991), Pyrrhocoridae (e. g., Calam & Scott 1969, Farine et al. 1992), and Rhopalidae (e. g., Aldrich et al. 1990, Davidová-Vilimová et al. in press). A review of all the published data on the persistence of the adult dorso-abdominal glands is prepared for publication (Davidová-Vilimová & Podoubský in press).

Sexual dimorphism

Dupuis (1949) described first sexual dimorphism in size of the adult anterior dorso-abdominal glands in Heteroptera. The paired anterior gland is much larger in male than in female of a predaceous representative of Asopinae (Pentatomidae), *Zicrona coerulea*. Later, Dupuis (1952, 1959) found dimorphism in two other asopine species, *Arma custos* and *Troilus luridus*. Age and sexual variation of the anterior dorso-abdominal glands was described in *Zicrona coerulea* by Dupuis (1952); the gland is much larger in males than in females and young larvae. The author did not find any dimorphism in the larvae of *Arma custos*, in which a distinct adult sexual dimorphism is also developed. Aldrich et al. (1978) reported, that a larval sexual dimorphism is not developed in two other asopine species with a conspicuously sexually dimorphic adult anterior gland, *Troilus luridus* and *Podisus maculiventris*.

A sexual dimorphism of the adult anterior dorso-abdominal gland is distinct, except of numerous Asopinae, in other pentatomoidean taxa. Gough et al. (1985) and Hamilton et al. (1985) described the paired anterior gland larger in male than in female, and reduced median and posterior glands with paired ostioles, in *Hotea gambiae* (Scutelleridae). Gough et al. (1986), Staddon et al. (1987), and Aldrich et al. (1990) confirmed this finding. Gough et al. (1986) described the same dimorphism in another scutellerid, *Sphaerocoris annulus*. James & Warren (1989) observed conspicuous sexual dimorphism of the anterior dorso-abdominal gland, larger in male, in *Biprorulus bibax* Breddin, 1900 (Pentatomidae). This result was corroborated by James & Mori (1995) and James et al. (1996). Davidová-Vilimová (1992) noted obvious sexual dimorphism of the anterior gland in two plataspid species, *Coptosoma mucronatum* and *C. scutellatum*.

A different type of sexual dimorphism was found in the adult anterior dorso-abdominal gland of *Nezara viridula* (Linnaeus, 1758) (Pentatomidae) by Lucchi & Solinas (1990) and Lucchi (1993). Sexual differences in histology and physiology as well as size dimorphism (the gland slightly larger in female) was described by Aldrich et al. (1978).

Numerous examples of a sexual dimorphism of the adult anterior gland have been described in frequently studied Asopinae and findings were often applied in their control. Aldrich et al. (1978) has published the most important study on *Podisus maculiventris* (Say, 1832), representing a model species with enormous sexual dimorphism (the male gland considerably larger than the female one). Aldrich et al. (1986a, 1991, 1997) and Aldrich (1995) mentioned other *Podisus* Herrich-Schaeffer, 1851 species with a similar sexual dimorphism: *P. distinctus* Stål, 1858; *P. fretus* Olsen, 1916; *P. mucronatus* Uhler, 1870; *P. nigrospinus* (Dallas, 1851); *P. placidus* Uhler, 1870; *P. rostralis* Stål, 1858; and *P. sagitta* (Fabricius, 1794). Aldrich (1995) and Aldrich et al. (1986b) recognized sexual dimorphism also in other genera, *Alcaeorrhynchus* Bergroth, 1891; *Oechalia* Stål, 1862; *Supputius* Distant, 1889; and *Tynacantha* Dallas, 1851.

Aldrich et al. (1984) and Aldrich (1995) described and illustrated conspicuous abdominal tergal sutures which are associated with the adult anterior dorso-abdominal gland in *Podisus maculiventris*. The sutures run longitudinally from the anterior ostioles, and their pattern is obviously sexually dimorphic. The sutures are developed between the terga 4–5 in female, and between the terga 4–7 in male and are supposed to channel secretion laterally from the ostioles.

Adult sexual dimorphism in the dorso-abdominal glands was recognized so far only in two other heteropteran families; a conspicuous dimorphism in Reduviidae (*Pristhesancus plagipennis* Walker, 1873 – Aldrich 1991) and slight one in Rhopalidae (*Corizus hyoscyami* (Linnaeus, 1758) – Davidová-Vilimová et al. in press). Aldrich (1995) summarized the reports on sexual dimorphism of the adult dorso-abdominal glands in Heteroptera, Scutelleridae, Pentatomidae: Asopinae, and Reduviidae; while Aldrich (1988b, 1996) listed all the known asopine species showing a sexual dimorphism of the anterior adult dorso-abdominal gland.

Staddon (in press) has studied the presence in cuticular preparations of ducted secretory units (= ductules) in the adult dorso-abdominal glands in both sexes of several European Pentatomoidea. The presence of ductules can indicate but not evidence the gland functionality. The author emphasized that the ductules might be present even if they were not actually observed. The pattern of paired, and probably functional, anterior gland with numerous ductules, together with the unpaired median and posterior glands with sparse ductules, was defined as basic for Pentatomoidea adults. The following three apomorphies were recognized: The loss of gland function, absent ductules; acquisition of a sexual dimorphism by the anterior gland; enhanced function of the median and posterior glands, with numerous ductules.

Function

Gupta (1961, 1964), Staddon (1979), and particularly Aldrich (1988a) summarized for Heteroptera different functions of scent gland secretion. Exocrine secretion from the larval dorso-abdominal and the adult metapleural scent glands evolved originally as chemical defence against microbial (e. g., Roth, 1961), vertebrate and invertebrate enemies. However, the sexual function predominated successively the original defensive and repellent role. Especially, the hypertrophied male anterior dorso-abdominal gland represents the source of sex pheromone in some asopines. The secretion products can control also other functions in aggregation or alarm behaviour. But the exploitation of these chemical signals by parasitoids and predators is at the same time disadvantage concerning the use of gland secretion in heteropteran chemical communication.

The development of the adult sexually dimorphic dorso-abdominal gland in predaceous asopine species was explained sufficiently by Aldrich et al. (1978, 1984), and Aldrich (1988a). It represents either an adaptation important for the reproductive aggregation in predatory species (more dispersed than phytophagous species), or an adaptation of males aimed to resist the predatory instincts of females. Secretion from the male anterior gland attracts both larvae and adults (Aldrich et al. 1984); males continue to release this secretion also during courtship. Secretion apparently func-

tions as a long-range attractant pheromone, as well as a short-range mating stimulant. Probably, males first search for food and then they attract mates. Female exocrine secretion from the anterior gland probably acts only over short distances, so that males can recognize females and their willingness to mate.

Gough et al. (1985) clarified the persistence of the adult dorso-abdominal glands in phytophagous species. The secretion of the anterior gland is mostly composed of isoprenoids, and "the need of isoprenoid defence, in addition to the more usual carbonyl defence [from metapleural glands], perhaps explains the retention of the gland in adult [of *Hotea gambiae*], which has suffered widespread reduction in Pentatomoidea."

Hamilton et al. (1985) studied chemistry of the secretion from the sexually dimorphic adult anterior dorso-abdominal gland in phytophagous *Hotea gambiae*. Commonly, it is agreed that the main function of the adult dorso-abdominal glands is an ecological one of the defense against predators. Various hypotheses have been proposed to explain the biological significance of sexual dimorphism of these glands but none has been confirmed yet. The probable function of anterior gland secretion in *H. gambiae* is defense perhaps including ovicidal defense against parasitoids (Diptera: Tachinidae: Phasiinae). Some components of the secretion could also have a sexual pheromonal role, to reduce interference of mating pairs by unmated males searching for a female. The authors proposed another explanation of the dimorphism. The male is in the greater need of chemical defense against predators than the female perhaps because of the sex differences in apparency or longevity. Generally, according to the authors, differences in the anterior gland between the sexes can be described as follows: the anterior gland is not hypertrophied in the male, rather it is reduced in the female, to compare with the larvae. Therefore, the simplest explanation of dimorphism is that the reduction of the female gland is related to her greater metabolic needs for reproduction.

Aldrich et al. (1990) demonstrated the function of the persistent adult dorso-abdominal glands in phytophagous Rhopalidae, assisted by chemical analysis of secretion. The median gland functions both as the repellent or pheromonal gland (aggregation, species specific communication). The posterior one, if functional, has analogical functions.

Secretion in larval exuviae

Kershaw & Muir (1907) observed remnants of the dorso-abdominal glands still full of secretion, in exuviae of the 5th larvae of *Tessaratomia papillosa* (Drury, 1770) (Tessaratomidae). Aldrich et al. (1984) and Aldrich (1988a, 1995) found that the gland contents are shed with the exuviae in Asopinae, Heteroptera and Pentatomoidea, respectively. Aldrich et al. (1993) used the gland content from larval exuviae for chemical analysis in two pentatomids, *Nezara viridula* and *Podisus nigrospinus* (as *P. connexivus*). The secretion can function as a kairomone for Tachinidae parasitizing newly moulted larvae (Aldrich et al. 1984).

Androconia

Carayon (1984) described as a new type of the integumentary unicellular glands, the androconia, of several Scutelleridae. The author described the paired patches containing the androconial glands, with cuticle sculptured differently than the main abdominal venter, in males of the following genera, *Irochrotus* Amyot et Serville, 1843, *Odontoscelis* Laporte, 1832, *Psacasta* Germar, 1839, and *Tectocoris* Hahn, 1834. No complete description and/or illustration of the two *Odontoscelis* species studied was given, except of SEM photos of the detailed patch structure and histological data of *Odontoscelis dorsalis* (Fabricius, 1803) and *Odontoscelis fuliginosa*. Knight et al. (1985) described the androconia and the chemical composition of the gland secretion in the male of *Tectocoris diophthalmus* Stål, 1870. The authors agreed with Carayon's (1984) explanation of androconial

function. Presuming that as pheromonal glands they produce an aphrodisiac, to be released during courtship when the androconial glands of the male brush against the female body.

The morphological state of the dorso-abdominal scent glands in adults (43 species) and larvae (26 species) of central European Pentatomoidea was described by the junior author during his Master's thesis study. The pattern of the androconia, the other type of heteropteran exocrine gland, was studied in scutellerid *Odontoscenus fuliginosa*. The aims of our study were to compare the gland pattern of the 5th larva with the adult, to estimate how rare or common is the persistence and the development of a sexual dimorphism in the dorso-abdominal glands in the adults. This paper should contribute to the hypothesis concerning the value and function of the dorso-abdominal glands in adults, with particular respect to sexual dimorphism.

MATERIAL AND METHODS

Material

The adults of 43 species from 34 genera, and the 5th larvae of 26 species (only in *Storia lunata* 4th instar) from 23 genera were studied. Only adults were available of 11 species. The material is deposited in the collection of senior author, at Department of Zoology of Charles University in Prague.

Material examined

(A = adults, B = Bohemia, L = larvae, M = Moravia, S = Slovakia, code = map field code for faunistic grid mapping system, according to Buchar 1982)

Pentatomoidea

Plataspidae: localities see Davidová-Vilimová (1992). *Copiosoma mucronatum* Seidenstuecker, 1963 – L, A, *Copiosoma scutellatum* (Geoffroy, 1785) – L, A.

Acanthosomatidae: *Acanthosoma haemorrhoidale* (Linnaeus, 1758) – A, B, Jablonecké Paseky (5257), 5.9.1995, M, NP Podyjí, Šobes (7161), 19.6.1996. *Elasmostethus intersimilis* (Linnaeus, 1758) – L, A, B, Jablonecké Paseky (5257), 17.8., 23.8., 5.9., 11.9., 18.9.1995, B, Lučany nad Nisou (5257), 9.8.1995. *Elasmucha ferrugata* (Fabricius, 1787) – L, A, B, Oslov (6551), 16.6., 20.7.1996, B, Ruda [reserve] nr. Veselí n. Lužnicí (6854), 26–31.5.1996. *Elasmucha fieberi* (Jakovlev, 1864) – L, A, B, Jablonecké Paseky (5257), 26.5., 21.7., 5.9., 11.9., 18.9.1995, B, Lučany nad Nisou (5257), 9.8.1995, B, Velký Osek (58–5957), 6.7.1995, M, National Park Podyjí, Popice (7162), 18.7.1995.

Cydidae: Thyreocorinae: *Thyreocoris scarabaeoides* (Linnaeus, 1758) – A, B, Předměstí (5551–52), 15.5.1986, B, Zbraslav (6052), 4.5.1995, 27.4.1996, B, Ruda [reserve], nr. Veselí n. Lužnicí (6854), 30.5.–4.6.1994, 26–31.1996, M, Znojmo env. (7162), 2–4.6.1977. Cydninae: *Aethus flavicornis* (Fabricius, 1794) – L, A, B, Tuháň (5753), 15.8.1992. *Aethus nigrinus* (Fabricius, 1794) – A, S, Čenkov env., nr. Šturovo (8277), 2.6.1976, S, Tarbucka (7596), 16.10.1985. *Cydneus aterrimus* (Forster, 1771) – L, A, S, Zádlel nr. Rožnáva (7391), 14.19.6.1976, S, Kralovský Chlmec (7597), 12.7.1988. Scirtinae: *Legnotus limbosus* (Costa, 1852) – L, A, B, Robin (6051), 12.8.1977, B, Praha – Botanical garden Na Slupi (5952), 18.5.1996, B, Praha – Kunratický les [forest] (5952–53), 10.5., 18.5.1995, 13.5., 25.6., 13.7., 25.8.1996, B, Velký Osek (58–5957), 6.7.1995, B, Zbraslav (6052), 4.5.1995, B, Oslov (6551), 8–9.6.1996, B, Pačejov (6647), 13.6.1996, B, Ruda [reserve], nr. Veselí n. Lužnicí (6854), 26–31.5.1996. *Scirtus luctuosus* Mulsant et Rey, 1866 – A, B, Praha – Kunratický les [forest] (5952–53), 10.5.1995, 13.5., 3.7.1996, B, Zbraslav (6052), 4.5.1995. *Tritomegas bicolor* (Linnaeus, 1758) – L, A, B, Praha – Vinická [street] (5952), May 1991, 9.7.1991, 8.5.1995, B, Sulava nr. Černošice (6051), 2.5.1977. *Tritomegas sexmaculatus* (Rambur, 1842) – L, A, B, Tuháň (5753), 20.6.1996, M, Pavlavske kopce (7165–66), 6.9.1996, M, National Park Podyjí, Popice (7162), 5.9.1996, S, Kamenín (8177), 8.9.1995.

Pentatomidae: Podopinae: *Ancyrosoma leucogrammes* (Gmelin, 1789) – L, A, S, Hogešarok [hills] nr. Šturovo (8177), 11.–15.9.1995. *Graphosoma lineatum* (Linnaeus, 1758) – L, A, B, Černousy (4956), 18.8.1995, B, Praha – Kunratický les [forest] (5952–53), 17.–18.5.1995, 10.5.1996, B, Oslov (6551), 13.5.1989, B, Ruda [reserve] nr. Veselí n. Lužnicí (6854), 29.5.1995. *Podops nuncia* (Fabricius, 1775) – A, B, Lysá nad Labem (5754–55), 21.5.1986, M, Lednice (71–7266), 5.6.1976, M, Na Adamech [reserve], nr. Brno (7068), 17.4.1989, S, Bříná (8077), 21.10.1977. *Vilpianus galii* (Wolff, 1802) – L, A, M, Na Adamech [reserve], nr. Brno (7068), 21.6.1987, S, Hogešarok [hills] (8177), 8.6.1972, S, Kralovský Chlmec (7597), 8.–10.7.1953, 12.7.1988, S, Viničky (7596), 11.7.1988. Pentatominae: *Sciocoris* *Sciocoris cursitans* (Fabricius, 1794) – L, A, B, Tuháň

(5753), 15.8.1992, B., Velký Osek (58–5957), 6.7.1995, 5.8.1996, B., Zbraslav (6052), 4.5.1995. Aelini: *Aelia acuminata* (Linnaeus, 1775) – L. A. B., Černousy (4956), 18.8.1995, B., Jablonecké Paseky (5257), 26.5., 3.7., 23.8.1995, B., Velký Osek (58–5957), 6.7.1995, B., Zbraslav (6052), 4.5.1995, M., National Park Podyjí, Popice (7162), 18.7.1995. *Neottiglossa leporina* (Herrich-Schaeffer, 1830) – L. A. B., Ruda [reserve], nr. Veselí n. Lužnicí (6854), 29.5.–3.6.1996, M., National Park Podyjí, Popice (7162), 18.7.1995. *Neottiglossa pusilla* (Gmelin, 1789) – A. B., Jablonecké Paseky (5257), 4.8.1995, B., Praha – Kunratický les [forest] (5952–53), 12.10.1995, 25.6.1996, B., Velký Osek (58–5957), 6.7.1995, B., Ruda [reserve], nr. Veselí n. Lužnicí (6854), 26.–31.5.1996. Eysarcorini: *Eysarcoris aeneus* (Scopoli, 1763) – A. B., Černošice (6051, 6052), 20.5.1977, B., Ruda [reserve], nr. Veselí n. Lužnicí (6854), 24.–28.5.1995. *Eysarcoris fabricii* Kirkaldy, 1904 – L. A. B., Praha – Kunratický les [forest] (5952–53), 13.5., 25.8.1996. Carpororini: *Carpocoris fuscispinus* (Boheman, 1846) – L. A. B., Jablonecké Paseky (5257), 4.8.1995, B., Sněhov (5357), 29.4.1995, B., Praha – Kunratický les [forest] (5952–53), 17.5.1995, B., Tuháň (5753), 29.6.1995, B., Velký Osek (58–5957), 6.7.1995, 5.8.1996, B., Zbraslav (6052), 4.5.1995, B. Ruda [reserve], nr. Veselí n. Lužnicí (6854), 29.5.1995, 26.–31.5.1996, M., National Park Podyjí, Popice (7162), 18.7.1995. *Carpocoris pudicus* (Poda, 1761) – A. B., Černousy (4956), 18.8.1995, B., Jablonecké Paseky (5257), 18.9.1995, B., Zbraslav (6052), 4.5.1995, B., Ruda [reserve], nr. Veselí n. Lužnicí (6854), 29.5.–3.6.1996. *Dolycoris baccarum* (Linnaeus, 1758) – L. A. B., Černousy (4956), 18.8.1995, B., Frýdštejn (4956), 11.7.1995, B., Jablonecké Paseky (5257), 17.8., 5.9.1995, B., Lučany nad Nisou (5257), 9.8.1995, B., Praha – Kunratický les [forest] (5952–53), 2.5., 10.5.1995, B., Velký Osek (58–5957), 6.7.1995, 4.8.1996, 4.5., 26.5., 17.8., 5.9., 11.9., 18.9.1995, B., Praha – Kunratický les [forest] (5952–53), 13.5.1996. *Holcostethus vernalis* (Wolff, 1804) – L. A. B., Černousy (4956), 18.8.1995, B., Jablonecké Paseky (5257), 17.8., 23.8., 5.9.1995, B., Lučany nad Nisou (5257), 9.8.1995, B., Praha – Kunratický les [forest] (5952–53), 10.5., 17.5., 18.5.1995, 13.5., 25.6.1996, B., Praha – Viničná [street] (5952), 10.5.1996. *Palomena prasina* (Linnaeus, 1761) – L. A. B., Jablonecké Paseky (5257), 4.5., 26.5., 17.8., 5.9., 11.9., 18.9.1995, B., Praha – Kunratický les [forest] (5952–53), 13.5.1996. *Palomena viridissima* (Poda, 1761) – L. A. B., Praha – Kunratický les [forest] (5952–53), 2.5., 7.5.1995, 13.5., 25.8.1996, B., Tuháň (5753), 15.8.1992. *Rubiconia intermedia* (Wolff, 1811) – A. B., Černošice (6051–52), 20.5.1977, M., Pavlovská kopce (7165–66), 6.9.1996, S., Vihorlat, Vinné (7198), 30.5.1974. *Staria lunata* (Hahn, 1835) – L. (4th instar), A. M., National Park Podyjí, Popice (7162), 18.7.1996, M., Znojmo (7162), 23.5.1992. Strachini: *Eurydema oleracea* (Linnaeus, 1758) – L. A. B., Zbraslav (6052), 4.5.1995, B., Praha – Kunratický les [forest] (5952–53), 13.5.1995, B., Lučany nad Nisou (5257), 9.8.1995, B., Černousy (4956), 18.8.1995, B., Sněhov (5357), 24.9.1995. *Eurydema ornatum* (Linnaeus, 1758) – L. A. S., Hegyfarok [hills] nr. Štúrovo (8177), 13.–14.9.1995. Pentatomini: *Pentatoma rufipes* (Linnaeus, 1758) – L. A. B., Jablonecké Paseky (5257), 8.8.1996, B., Oslov (5551), 14.8.1996, M., National Park Podyjí, Ledové sluje (7160), 2.9.1996, M., National Park Podyjí, Popice (7162), 8.–13.6.1997, S., Vysoké Tatry Mts. (6886), 3.9.1977. *Piezodorus lituratus* (Fabricius, 1794) – L. A. B., Klecany (5852), 23.7., 27.8.1996, M., National Park Podyjí, Popice (7162), 5.9.1996. *Rhaphigaster nebulosa* (Poda, 1761) – L. A. B., Praha – Viničná [street] (5952), 29.10.1996, M., Valtice (7266), 18.4.1973, S., Kováčov nr. Štúrovo (8178), 1963, S., Štúrovo (81–8278), 19.5.1970, 3.9.1995, S., Tisa nr. V. Trakany (7698), 24.5.1973, Bulgaria or, Arktúto, 9.–13.6.1971. Asopini: *Arma custos* (Fabricius, 1794) – L. A. B., Jablonecké Paseky (5257), 4.8., 5.9., 11.9., 18.9.1995, 18.8.1996, M., Pavlovská kopce (7165–66), 6.9.1996. *Pteromeris bidens* (Linnaeus, 1758) – L. A. B., Neratovice env. (5357), 30.5.1987, B., Jablonecké Paseky (5257), 11.9., 18.9.1995, B., Oleško (5551), 6.10.1986, B., Pačejov (6647), 9.10.1996. *Rhacognathus punctatus* (Linnaeus, 1758) – A. B., Jablonecké Paseky (5257), 4.5., 26.5., 17.8.1995, 16.6.1996, B., Soos [reserve], nr. Františkovy Lázně (5840), 14.6.1987. *Troilus luridus* (Fabricius, 1775) – L. A. B., Jablonecké Paseky (5257), 4.8., 6.8., 17.8., 23.8., 11.9., 18.9.1995, 18.8.1996, M., Pohled (6359), 9.1911. *Zicrona coerulea* (Linnaeus, 1758) – L. A. B., Jablonecké Paseky (5257), 4.7., 17.–18.8.1995, B., Soos [reserve], nr. Františkovy Lázně (5840), 25.–26.5.1987.

Scutelleridae: *Eurygaster maura* (Linnaeus, 1758) – L. A. B., Frýdštejn (5356), 11.7.1995, B., Lučany nad Nisou (5257), 9.8.1995, B., Černousy (4956), 18.8.1995, B., Jablonecké Paseky (5257), 23.8., 11.9.1995, B., Velký Osek (58–5957), 6.7.1995, B., Ruda [reserve], nr. Veselí n. Lužnicí (6854), 26.–31.5.1996, M., Ječmenišťe nr. Znojmo (7262), 18.6.1996, M., National Park Podyjí, Popice (7162), 18.7.1995, 21.6.1996, M., Popická kopce [reserve] (7162), 18.6.1996. *Eurygaster testudinaria* (Geoffroy, 1785) – A. B., Pačejov (6647), 9.10.1996. *Odontoscels fuliginosa* (Linnaeus, 1761) – L. A. B., Klenec (5651), 9.6.1986, B., Předonín (5551–52), 15.5.1986, B., Karlštejn (6051), 5.6.1992, B., Nelahozeves (5751), 19.4.1996, B., Tišice (5753), 21.8.1986, M., National Park Podyjí, Popice (7162), 18.7.1995.

Methods

Study specimens were preserved in 75% ethanol or in Pampel's fluid. The specimens were dissected and drawn in distilled water. The dry adult specimens were kept for about 4 minutes in boiling 10% KOH, and then in distilled

water. The abdominal cavity was opened from the ventral side and all tissues surrounding the glands were removed with watchmaker forceps.

Terminology and common characters

The "transverse line" in larvae, a distinct transverse line, sometimes of different colouration than gland, on the surface of all three glands, dividing gland into anterior and posterior part, not always of the same size.

The ostioles of the glands are located in the intersegmental lines.

The terminology used by various authors to locate glands is considerably diverse, e.g. first, second, third, anterior, medial, posterior; 3-4, 4-5, 5-6; III-IV, IV-V, V-VI, and some others, including combinations of the above terms. We use the terms *anterior*, *median*, and *posterior*; the anterior gland is located beneath intersegmental line between the abdominal terga 3 and 4, the median gland between the terga 4 and 5, and the posterior gland between the terga 5 and 6.

We use a simple term *gland(s)* through the text in the sense of the dorso-abdominal scent gland(s).

We distinguish two types of the median and the posterior glands, according to their shape and location:

- a) *croissant gland* – transversally oval-shaped, following course of the depression, which connects the ostioles in the intersegmental line on the dorsal surface;
- b) *horn gland* – gland remnants, resembling elongated horns, connected by a narrow membranous stripe, located directly beneath the larval ostioles.

The different appearance of the median and the posterior glands, if developed, is described in detail in the text.

The median and the posterior glands are generally unpaired in the larvae and the adults of all the species studied.

The median and the posterior adult glands are very probably not functional, according to our morphological observations. They appeared as empty, wrinkled, colourless, membranous sacs, sometime are vestigial or difficult to distinguish.

RESULTS

Plataspidae

Coptosoma scutellatum, *C. mucronatum*

Larvae (adapted from Davidová-Vilimová, 1992: fig. 28). Three unpaired glands, deep orange to pinkish. Anterior gland reduced, completely covered by median gland. Median and posterior glands crosswise oval, conspicuous transverse lines developed. Shape and size depend on functional state, empty gland narrow, acute laterally, full gland almost spherical, rounded laterally. Adults (adapted from Davidová-Vilimová, 1992: figs 21, 22). Anterior gland paired in both sexes, in male larger than in female, reaching up to tergum II, approximately kidney-shaped; in female spherical, situated laterally next to ostioles. Median and posterior glands almost completely reduced, of croissant type, milky-white in both sexes.

Acanthosomatidae

Sexual dimorphism was not found in any species studied. Anterior gland in larvae and adults paired, median and posterior adult glands of croissant type in most of the species studied.

Acanthosoma haemorrhoidale (Figs 1, 2)

Larval material not available. Adults (Figs 1, 2). Anterior gland spherical, milky-white in both sexes. Median and posterior glands in male of horn type, in female of croissant type, anteriorly elongated; different shapes of posterior gland illustrated in Fig. 2.

Elasmotethus interstinclus (Figs 3, 4, 93)

Larvae (Fig. 93). Anterior gland of middle size, spherical, slightly depressed ventrally, pale ochre. Median and posterior glands transversally divided by thick wall into two colourless, structurally identical parts. Full glands in wide contact. Adults (Figs 3, 4). Anterior gland globular, slightly depressed, white in both sexes. Different shapes, probably representing full and empty glands, illustrated in Fig. 3.

Elasmucha fieberi (Figs 5, 6, 94)

Larvae (Fig. 94). Anterior gland of middle size, approximately oval, slightly flattened, white. Median and posterior glands pale orange, with deep orange transverse line. Median gland about 1/3 of size of posterior one. Adults (Figs 5, 6). Anterior gland of about the same size in both sexes, erythrocyte-shaped, white. Variability of gland shape in female illustrated in Fig. 6.

Elasmucha ferrugata (Figs 7, 8, 95)

Larvae (Fig. 95). Anterior gland of middle size, spherical shape and grey colour, contrary to previous species. Median gland oval, posterior gland trapezoidal, laterally pointed. Both glands orange, transverse lines developed. Adults (Figs 7, 8). Anterior gland the same as in *E. fieberi*.

Cydnidae

Sexual dimorphism not found in any species studied. All glands of almost all the studied species uniformly coloured, milky-white.

Cydinae

Larval anterior gland unpaired.

Aethus flavicornis (Figs 9, 10, 96)

Larvae (Fig. 96). Anterior gland oval, laterally strongly elongated, colourless; posterior part of gland overlapped by median gland in ventral view. Median and posterior glands oval, colourless; median a little larger than posterior. Adults (Figs 9, 10). Anterior gland not developed. Median and posterior glands of croissant type. Intersegmental membranes thickened in places of former larval evaporatoria on the ventral side of dorsum between terga IV and V, and V and VI.

Aethus nigrinus (Figs 11, 12)

Larval material not available. Adults (Figs 11, 12). The same condition as in *A. flavicornis*.

Cydus aterrimus (Figs 13, 14, 97)

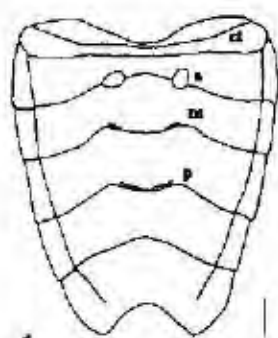
Larvae (Fig. 97). Anterior gland unpaired, with large lateral sacs. Median gland oval, laterally pointed, posterior gland oval, with anterior wall parallel to intersegmental line. Adults (Figs 13, 14). Anterior gland paired, spherical, small in both sexes. Median and posterior glands of horn type. Intersegmental membrane slightly thickened in places of former larval evaporatoria on ventral side of dorsum, between terga IV and V, and V and VI.

Schirinae

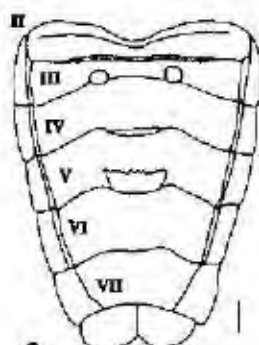
Legnotus limbosus (Figs 15, 16, 98)

Larvae (Fig. 98). Anterior gland paired, small, oval-shaped, pale pinkish. Median and posterior glands oval, with anterior walls parallel to intersegmental lines, median larger than posterior. Adults (Figs 15, 16). Anterior gland unpaired, dumb-bell-shaped in male, sponge-biscuit-shaped in female. Median and posterior glands of croissant type in both sexes.

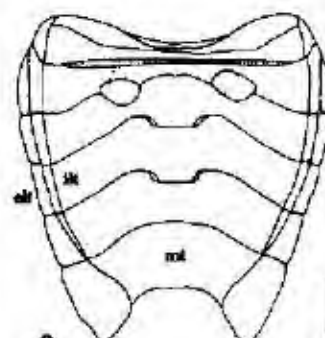
Figs 1–12 Dorsal-abdominal scent glands of adults, ventral view. 1, 2 – *Acanthosoma haemorrhoidale* (Linnaeus). 3, 4 – *Elasmosteethus interstinctus* (Linnaeus). 5, 6 – *Elasmucha fieberi* (Jakovlev). 7, 8 – *Elasmucha ferrugata* (Fabricius). 9, 10 – *Aethus flavicornis* (Fabricius). 11, 12 – *Aethus nigrinus* (Fabricius) odd – male, even – female; a – anterior gland, ct – cuticular ledge, elt – external laterotergite, il – intersegmental line, int – internal laterotergite, m – median gland, mt – mediotergite, p – posterior gland, II–VII – abdominal mediotergite II–VII; dotted area – membranous intersegmental area, hatched area – strongly pigmented and sclerotized parts, dotted line – variable shape of anterior gland. Scale – 1 mm.



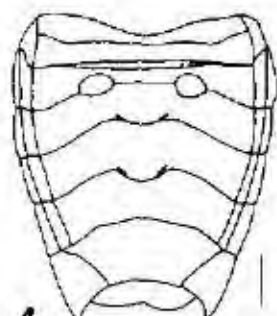
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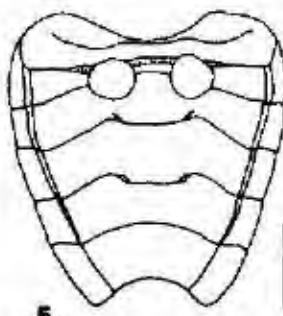
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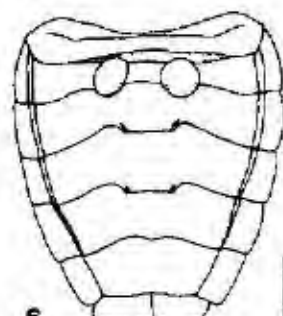
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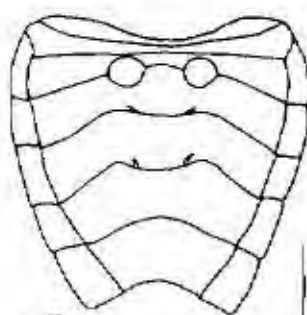
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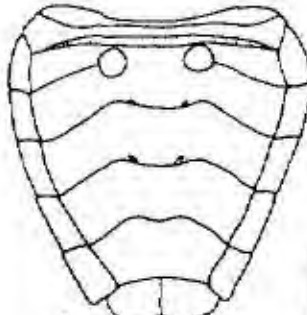
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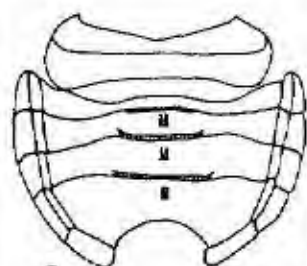
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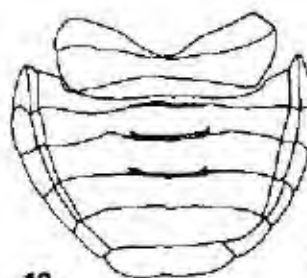
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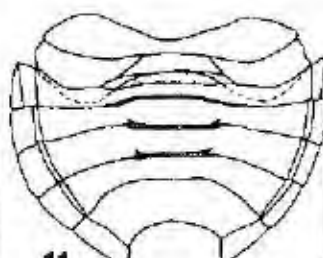
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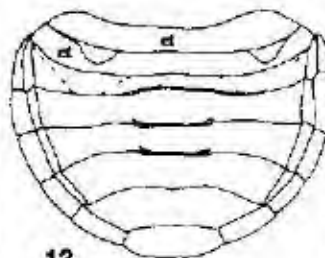
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12

Sehirus luctuosus (Figs 17, 18)

Larval material not available. Adults (Figs 17, 18). Anterior gland paired, globular, slightly smaller in male than in female. Median and posterior glands of croissant type in both sexes.

Tritomegas bicolor (Figs 19, 20, 99)

Larvae (Fig. 99). Anterior gland paired, spherical; sacs situated conspicuously submedially. Median and posterior glands small, oval. Adults (Figs 19, 20). Anterior gland unpaired, in contrary to larvae; dumb-bell-shaped in male, sponge-biscuite shaped in female; slightly larger in female than in male. Median and posterior glands of croissant type, conspicuously oblong in both sexes.

An endoparasitic larva, so far unidentified specifically, belonging probably to Tachinidae (Diptera) was found inside the abdomen of a female (Fig. 20). The larva was found beneath two small holes in the cuticle anteriorly and posteriorly to the intersegmental line III-IV, near to the anterior gland. The cuticle around the holes is conspicuously sclerotized (marked "scars" in Fig. 20).

Tritomegas sexmaculatus (Figs 21, 22, 100)

Larvae (Fig. 100). Anterior gland unpaired, two conspicuous lateral sacs connected by narrow median tissue bridge. Median and posterior glands oblong, conspicuously small. Adults (Figs 21, 22). Anterior gland unpaired, dumb-bell-shaped, small in both sexes. Median and posterior glands of croissant type, rounded.

Thyreocorinae

Thyreocoris scarabaeoides (Figs 23, 24)

Larval material not available. Adults (Figs 23, 24). Anterior gland unpaired, oval, elongated laterally. Conspicuous membranous strip between terga III and IV developed. Anterior gland distinctly visible only in posteroventral view. Median and posterior glands not developed. Intersegmental membranes thickened in areas of former larval evaporatoria on ventral surface of abdominal dorsum, between terga IV and V, and V and VI.

Pentatomidae

Podopinae

Anterior gland of larvae generally paired. Colour of glands mostly uniformly white, originated probably after dying of material.

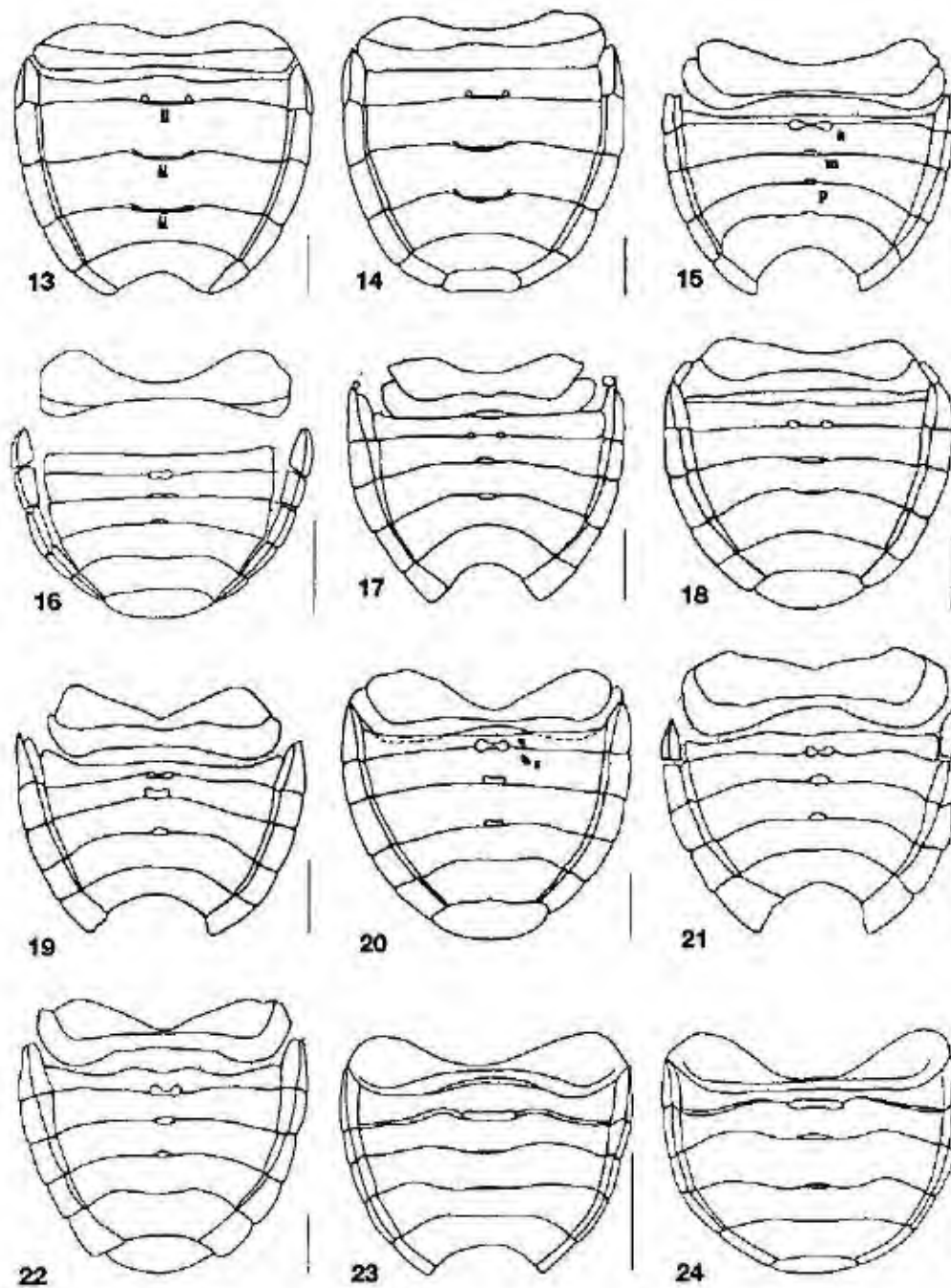
Alpianus galii (Figs 25, 26, 101)

Larvae (Fig. 101). Anterior gland very small, spherical, colourless. Median and posterior glands oval, orange. Adults (Figs 25, 26). Anterior gland paired, small, spherical in both sexes. Median and posterior glands of croissant type.

Podops inuncta (Figs 27, 28)

Larval material not available. Adults (Figs 27, 28). Anterior gland paired, about two times larger in male than in female, broadly oval in male, oval in female. Median and posterior glands not developed in both sexes.

Figs 13-24. Dorsal-abdominal scent glands of adults, ventral view. 13, 14 - *Cydnius aterrimus* (Forster), 15, 16 - *Leptogaster limbosus* (Costa), 17, 18 - *Sehirus luctuosus* Mulsant et Rey, 19, 20 - *Tritomegas bicolor* (Linnaeus), 21, 22 - *Tritomegas sexmaculatus* (Rambur), 23, 24 - *Thyreocoris scarabaeoides* (Linnaeus). odd - male, even - female; a - anterior gland, il - intersegmental line, m - median gland, p - posterior gland, s - scar; dotted area - membranous intersegmental area, hatched area - strongly pigmented and sclerotized parts. Scale - 1 mm.



Graphosoma lineatum (Figs 29, 30, 102)

Larvae (Fig. 102). Anterior gland very small, oval; gland sacs situated more medially than lateral margins of median gland. Median gland oval to trapezoidal. Posterior gland larger than median, trapezoidal, elongated posteriorly. All glands brightly orange; transverse lines developed in median and posterior glands. Adults (Figs 29, 30). Anterior gland paired; spherical to slightly oval, milky-white. Median and posterior glands of croissant type in both sexes.

Ancyrosoma leucogrammes (Figs 31, 32, 103)

Larvae (Fig. 103). Anterior gland spherical, white, sacs situated more laterally than lateral margins of median gland. Median and posterior glands small, oval. Adults (Figs 31, 32). Anterior gland paired, oval in both sexes. Median and posterior glands of croissant type in both sexes.

Pentatominae

Relative uniformity of shape, size and position of the glands observed in Pentatominae. Larval and adult anterior glands always paired, small. Median and posterior glands of larvae and adults always unpaired, in adults of croissant type. *Sciocoris cursitans* (Sciocorini) was selected as a model species for the whole subfamily, and described in detail. The other species are compared with the model pattern ("as in *S. cursitans*" in the following text), and only different states are described in more detail.

Sciocorini

Sciocoris cursitans (Figs 33, 34, 104)

Larvae (Fig. 104). Anterior gland paired, small, spherical. Median and posterior glands oval, bluntly pointed laterally, distinct transverse lines deeply orange. Posterior gland elongated caudally and partially overlapped by posterior part of median gland in ventral view. All glands orange. Adults (Figs 33, 34). Anterior gland paired, small, spherical, orange. Median and posterior glands of croissant type in both sexes, usually transversally oval, fitting the depression in corresponding intersegmental line.

Aeliini

Aelia acuminata (Figs 35, 36, 105)

Larvae (Fig. 105). Anterior gland as in *S. cursitans*. Median and posterior glands trapezoidal, elongated caudally. Small posterior part of median gland overlapped by anterior part of posterior gland in ventral view. Adults (Figs 35, 36). As in *S. cursitans*. Anterior gland slightly larger in male than in female.

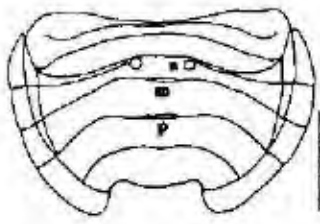
Neottiglossa leporina (Figs 37, 38, 106)

Larvae (Fig. 106). Anterior gland small, spherical, lightly orange. Median and posterior glands spindle-shaped, conspicuously elongated laterally, transverse lines developed, glands in contact. Adults (Figs 37, 38). As in *S. cursitans*.

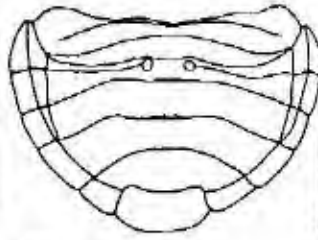
Neottiglossa pusilla (Figs 39, 40)

Larval material not available. Adults (Figs 39, 40). Anterior gland oval; in female slightly larger than in male. Median and posterior glands as in *S. cursitans*.

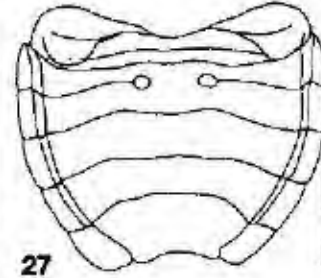
Figs 25-36 Dorso-abdominal scent glands of adults, ventral view. 25, 26 - *Vilpianus galii* (Wolff), 27, 28 - *Podops uncta* (Fabricius), 29, 30 - *Graphosoma lineatum* (Linnaeus), 31, 32 - *Ancyrosoma leucogrammes* (Gmelin), 33, 34 - *Sciocoris cursitans* (Fabricius), 35, 36 - *Aelia acuminata* (Linnaeus) odd - male, even - female; a - anterior gland, m - median gland, p - posterior gland, dotted area - membranous intersegmental area. Scale - 1 mm.



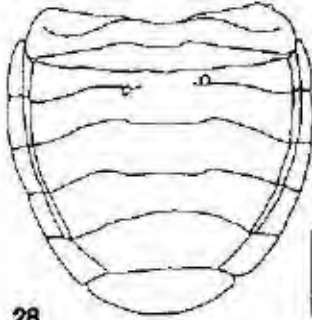
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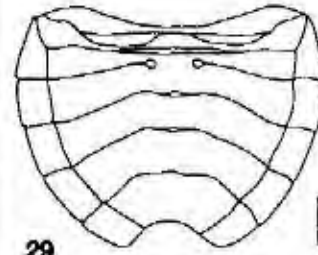
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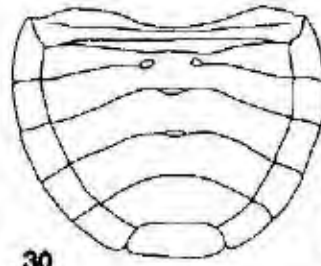
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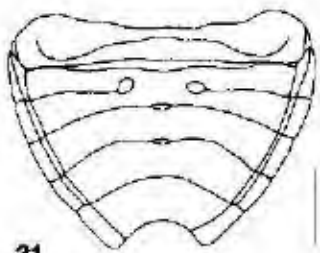
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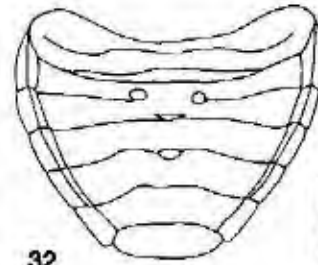
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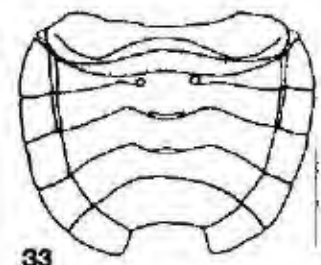
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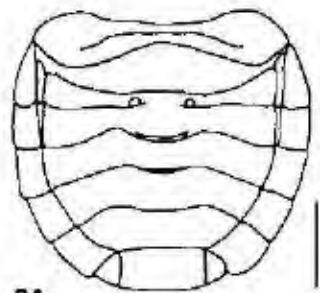
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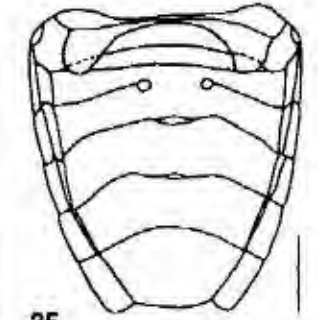
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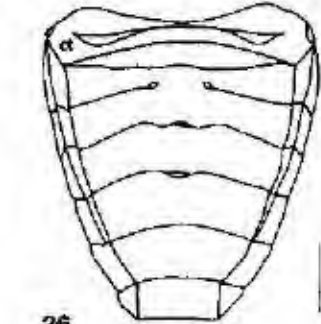
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Eysarcorini

Eysarcoris aeneus (Figs 41, 42)

Larval material not available. Adults (Figs 41, 42). Anterior gland spherical, small in male, about four times smaller than in female, colourless (probably because the material was dried). Median and posterior glands large.

Eysarcoris fabricii (Figs 43, 44, 107)

Larvae (Fig. 107). Anterior gland small, spherical. Median gland elliptical, wide transverse line developed. Posterior gland elliptical, transverse line forming cranial margin of gland in ventral view; anterior part of gland conspicuously small. All glands colourless, transverse lines orange. Adults (Figs 43, 44). As in *S. cursitans*. Anterior gland of the same size in both sexes.

Carpocorini

Rubiconia intermedia (Figs 45, 46)

Larval material not available. Adults (Figs 45, 46). As in *S. cursitans*. Anterior gland ochre, median and posterior glands pale red.

Staria lunata (Figs 47, 48, 108)

Larvae (4th instar). Anterior gland small, spherical, white, overlapped by anterior part of median, almost spherical gland. Posterior gland oval, partly overlapped by posterior part of median gland. Both glands orange with dark orange transverse lines. Adults (Figs 47, 48). As in *S. cursitans*.

Dolycoris baccarum (Figs 49, 50, 109)

Larvae (Fig. 109). Anterior gland small, drop-shaped. Median and posterior glands elliptical, pointed laterally, in contact, distinct, dark orange transverse lines developed. All glands orange. Adults (Figs 49, 50). As in *S. cursitans*.

Holcostethus vernalis (Figs 51, 52, 110)

Larvae (Fig. 110). Anterior gland small, spherical, white. Median gland almost spherical, transverse line developed. Posterior gland oval, partly overlapped anteriorly by posterior part of median gland. Both glands orange. Adults (Figs 51, 52). As in *S. cursitans*.

Carpocoris fuscispinus (Figs 53, 54, 111)

Larvae (Fig. 111). Anterior gland small, spherical. Median gland elliptical, posterior trapezoidal, elongated posteriorly; both glands orange, dark orange transverse lines developed. Adults (Figs 53, 54). As in *S. cursitans*; anterior gland small, slightly larger in female than in male.

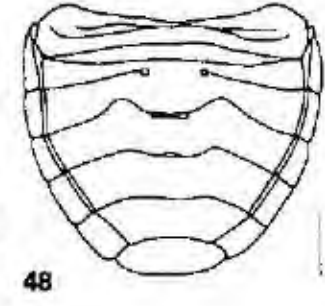
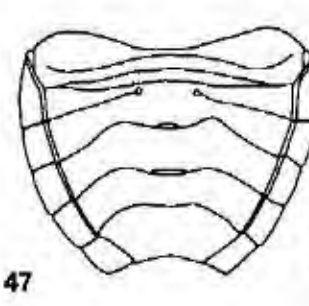
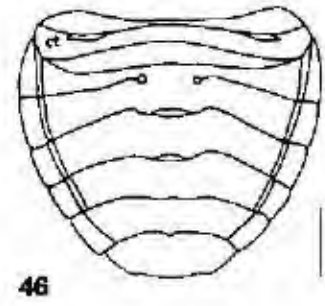
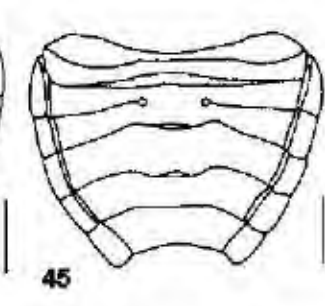
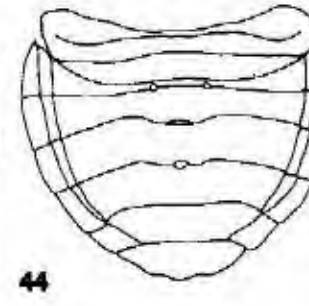
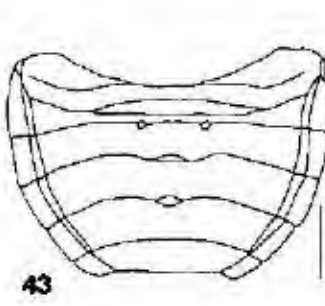
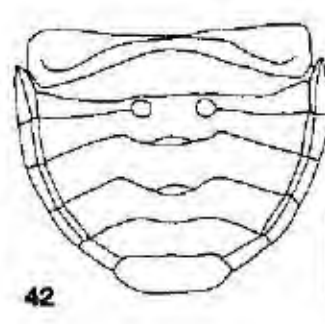
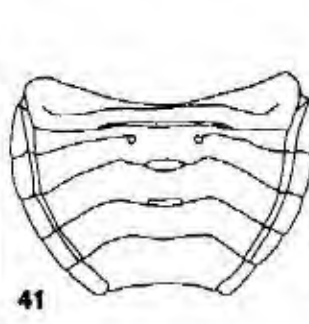
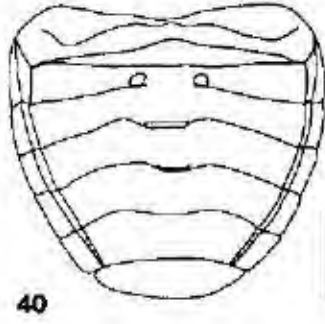
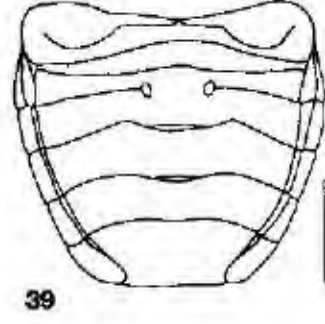
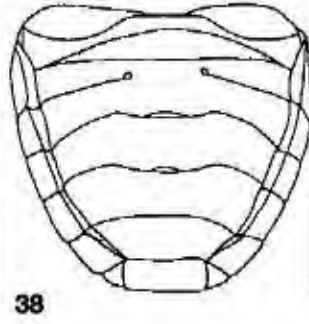
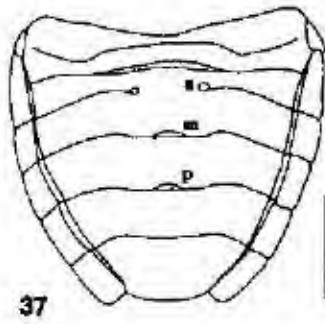
Carpocoris pudicus (Figs 55, 56)

Larval material not available. Adults (Figs 55, 56). As in *S. cursitans*.

Palomena prasina (Figs 57, 58, 112)

Larvae (Fig. 112). Anterior gland small, spherical, white. Median gland elliptical, posterior part of gland curved out laterally. Posterior gland elliptical, pointed laterally. Both glands with transverse lines. All glands orange. Adults (Figs 57, 58). As in *S. cursitans*.

Figs 37–48. Dorsal-abdominal scent glands of adults, ventral view. 37, 38 – *Neottiglossa leporina* (Herrich-Schäffer), 39, 40 – *Neottiglossa pusilla* (Gmelin), 41, 42 – *Eysarcoris aeneus* (Scopoli), 43, 44 – *Eysarcoris fabricii* Kirkaldy, 45, 46 – *Rubiconia intermedia* (Wolff), 47, 48 – *Staria lunata* (Hahn). odd – male, even – female; a – anterior gland, m – median gland, p – posterior gland, dotted area – membranous intersgmental area. Scale – 1 mm.



Palomena viridissima (Figs 59, 60, 113)

Larvae (Fig. 113). Anterior gland conspicuously small, spherical, milky-white. Median and posterior glands oval, pointed laterally, transverse lines pale yellow. Adults (Figs 59, 60). As in *S. cursitans*.

Strachiini

Eurydema oleracea (Figs 61, 62, 114)

Larvae (Fig. 114). Anterior gland oval, white, larger than gland in other pentatomine species studied. Median and posterior glands elliptical, pointed laterally, median larger than posterior, transverse lines orange. Adults (Figs 61, 62). Anterior gland spherical, orange; in female almost twice as large as in male. Median and posterior glands in male twice as large as in female.

Eurydema ornatum (Figs 63, 64, 115)

Larvae (Fig. 115). Anterior gland small, spherical, milky-white. Median and posterior glands trapezoidal, transverse lines orange, posterior gland smaller than median, median gland with anterior margin slightly concave, posterior gland with posterior margin conspicuously concave medially. Adults (Figs 63, 64). Anterior gland similar to *E. oleracea*, spherical, orange; in female about twice as large as in male. Median and posterior glands as in *S. cursitans*.

Pentatomini

Pentatoma rufipes (Figs 65, 66, 118)

Larvae (Fig. 118). Anterior gland elliptical, pointed laterally, conspicuously smaller than median gland. Posterior gland trapezoidal. All glands orange. Adults (Figs 65, 66). Anterior gland larger than corresponding gland in the other pentatomine species studied, oval, orange. Median and posterior glands large, beige.

Raphigaster nebulosa (Figs 67, 68, 116)

Larvae (Fig. 116). Anterior gland small, oval, white. Median gland elliptical, elongated posteriorly, transverse line wide. Posterior gland roughly trapezoidal, transverse line developed. Both glands orange. Adults (Figs 67, 68). As in *S. cursitans*.

Piezodorus lituratus (Figs 69, 70, 117)

Larvae (Fig. 117). Anterior gland spherical, white. Median gland about semicircular. Posterior gland elliptical; glands orange, in contact, transverse lines developed. Adults (Figs 69, 70). As in *S. cursitans*, with median and posterior glands large, in female slightly larger than in male.

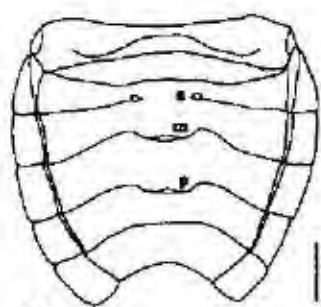
Asopinae

Conspicuous sexual dimorphism in both shape and size in anterior gland in larvae and/or adults is developed in some of the representatives of subfamily.

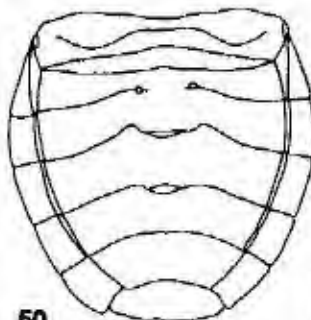
Picromerus bidens (Figs 71, 72, 119)

Sexual dimorphism not developed. Larvae (Fig. 119). Anterior gland paired, spherical; median and posterior unpaired. All glands reddish. Median gland elliptical, elongated posteriorly; posterior slightly smaller than median. Adults (Figs 71, 72). Anterior gland paired, small, spherical, brightly red (sometime, due to long fixation, milky-white). Median and posterior glands of croissant type, rudimental, milky-white.

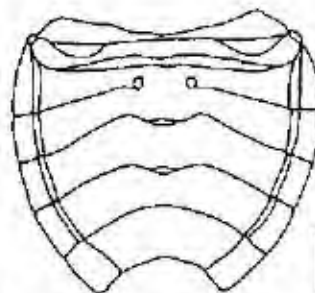
Figs 49–60. Dorsal-abdominal scent glands of adults, ventral view. 49, 50 – *Dolycoris baccarum* (Linnaeus), 51, 52 – *Holcostethus vernalis* (Wolff), 53, 54 – *Carpocoris fuscispinus* (Boheman), 55, 56 – *Carpocoris pudicus* (Poda), 57, 58 – *Palomena prasina* (Linnaeus), 59, 60 – *Palomena viridissima* (Poda) odd – male, even – female; a – anterior gland, m – median gland, p – posterior gland, dotted area – membranous intersegmental area. Scale – 1 mm.



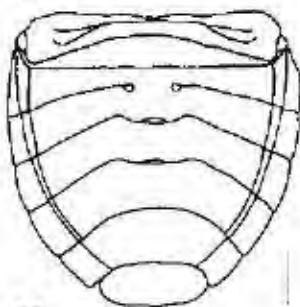
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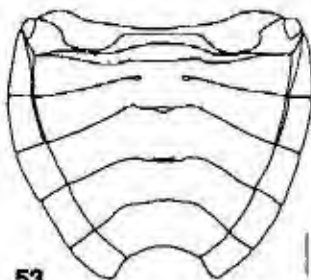
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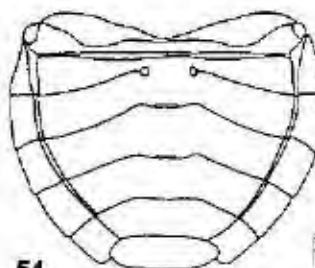
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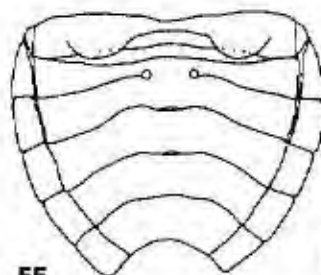
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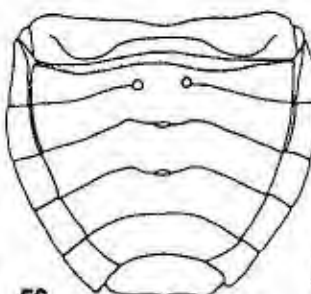
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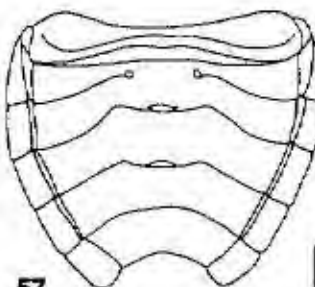
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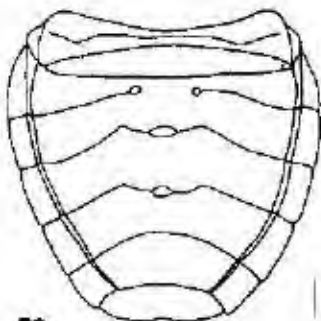
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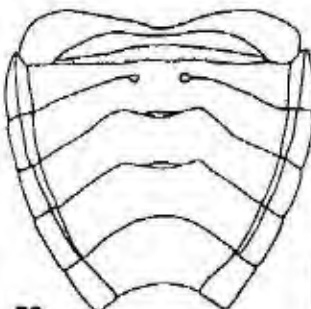
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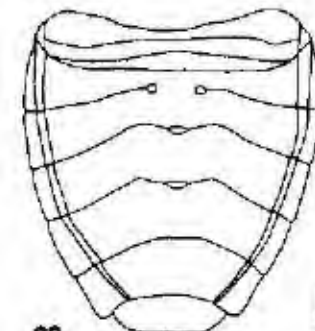
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Arma custos (Figs 73, 74, 89, 90)

Conspicuous sexual dimorphism in anterior gland developed in both larvae and adults. Larvae (Figs 89, 90) Male. Anterior gland paired, about ten times larger than in female, grey, slightly dorsoventrally flattened, posteriorly partly overlapping anterior part of median gland. Median and posterior glands orange, oval. Female. Anterior gland paired, small, almost spherical, orange, median and posterior glands trapezoidal, bright orange. Adults (Figs 73, 74) Male. Anterior gland paired, conspicuously hypertrophied, shape variable due to large size, mostly oval, slightly elongated posteriorly (two variations of shape illustrated in Fig. 73), dorsoventrally flattened, anteriorly not reaching anterior margin of tergum III, posteriorly reaching, and more or less overlapping tergum V and median gland. Surface of gland granulated, orange. Median and posterior glands of croissant type, white. Female. Anterior gland paired, of middle size, about 1/4 to 1/5 the size of male gland, dorsoventrally flattened, with granulated surface, white. Median and posterior glands same as in male.

Troilus luridus (Figs 75, 76, 120)

Conspicuous sexual dimorphism of anterior gland is developed only in adults. Larvae (Fig. 120) Anterior gland paired, small, orange. Median and posterior glands oval to almost globular, pale orange, in contact. Adults (Figs 75, 76) Male. Anterior gland paired, conspicuously hypertrophied (left sac partly empty illustrated in Fig. 75), shape variable, surface granulated, orange to pinky. Median and posterior glands strongly reduced, of croissant type, sometimes poorly visible. Female. Anterior gland paired, conspicuously small, about 1/20 the size of male gland, spherical, orange. Median and posterior glands same as in male.

Rhacognathus punctatus (Figs 77, 78)

Sexual dimorphism not developed. Larval material not available. Adults (Figs 77, 78) Anterior gland paired, small, spherical, brightly red. Median and posterior glands of croissant type, rudimental, milky white.

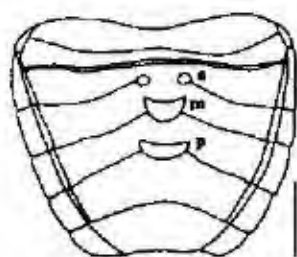
Zicrona coerulea (Figs 79, 80, 91, 92)

Conspicuous sexual dimorphism of anterior gland developed in both larvae and adults. Larvae (Figs 91, 92) Anterior gland paired, in male conspicuously large and strongly dorsoventrally flattened, beige, in female small, orange, but not well seen because of merging with surrounding fat body. Median and posterior glands trapezoidal, brightly orange, in contact. Adults (Figs 79, 80) Male. Anterior gland paired, hypertrophied, of highly variable shape, in one specimen posterior margins of gland sacs reach even tergum VI, dorsoventrally flattened, surface granulated, pink. Median and posterior glands of croissant type, reduced, colourless. Female. Anterior gland paired, very small, about 1/20 to 1/25 of size of male gland, spherical, red. Median and posterior glands same as in male.

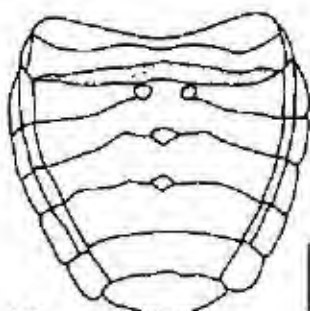
Scutelleridae

Sexual dimorphism not found in any species studied. Anterior gland of both larvae and adults paired.

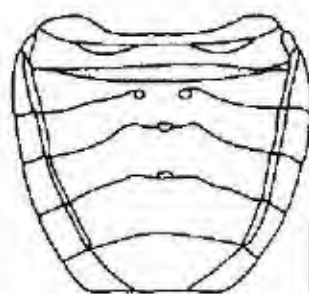
Figs 61-72. Dorsal abdominal scent glands of adults, ventral view. 61, 62 - *Eurydema oleracea* (Linnaeus), 63, 64 - *Eurydema ornatum* (Linnaeus), 65, 66 - *Pentatomia rufipes* (Linnaeus), 67, 68 - *Rhaphigaster nebulosa* (Poda), 69, 70 - *Piezodorus lituratus* (Fabricius), 71, 72 - *Pteromerus bidens* (Linnaeus). odd - male, even - female. a - anterior gland, il - intersegmental line, m - median gland, p - posterior gland, dotted area - membranous intersegmental area, hatched area - strongly pigmented and sclerotized area. Scale - 1 mm.



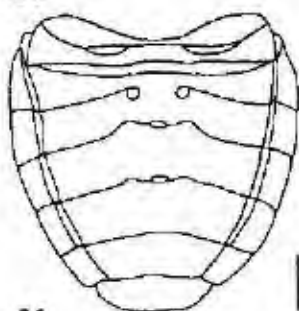
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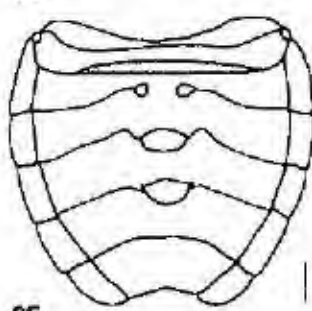
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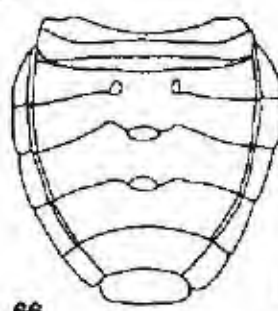
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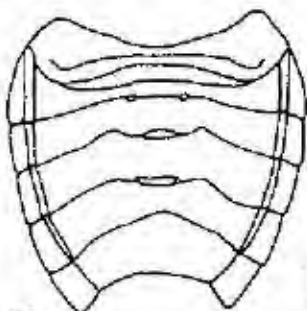
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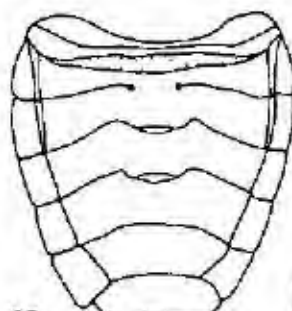
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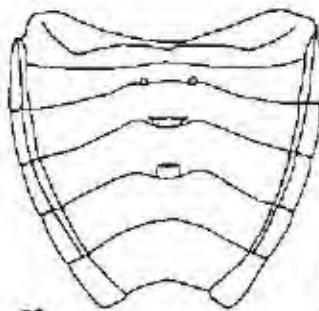
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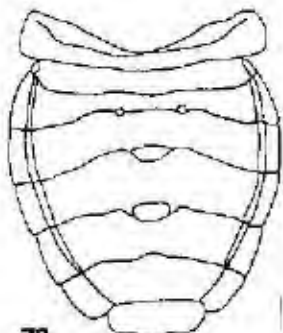
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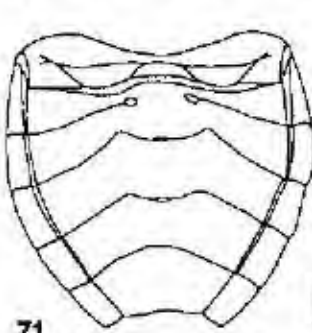
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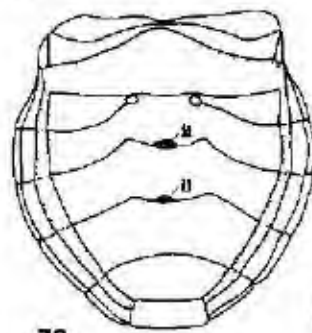
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Eurygaster maura (Figs 81, 82, 121)

Larvae (Fig. 121). Anterior gland small, spherical, situated conspicuously medially. Median and posterior glands elliptical, pointed laterally. All glands orange, conspicuous, deeply orange transverse lines developed. Adults (Figs 81, 82). Anterior gland situated conspicuously sublaterally, spherical, small, its size roughly conforming only to diameter of ostiole; brightly red. Median and posterior glands of croissant type, orange.

Eurygaster testudinaria (Figs 83, 84)

Larval material not available. Adults (Figs 83, 84). As in *E. maura*, milky-white.

Odontoscelis fuliginosa (Figs 85, 86, 122)

Larvae (Fig. 122). Anterior gland situated distinctly laterally, more than in larvae of the other families studied, of middle size, spherical, brightly red. Median and posterior glands transversally oval, brightly pink. All glands with granulated surface. Adults (Figs 85, 86). Anterior gland large, only slightly smaller than in larvae, spherical, orange. Median and posterior glands large, milky-white, resembling empty membranous sacs.

Dorso-abdominal glands of an imperfect specimen of *Holcostethus vernalis* (Figs 123, 124) 5th larva

Glands probably functional, though abdominal cuticle was injured. Paired anterior gland and evaporatorium conspicuously damaged, only left, small, sac-shaped gland and part of evaporatorium developed. Unpaired median gland and evaporatorium less damaged, sac-shaped gland asymmetrical, only left evaporatorial ostiole developed. Unpaired posterior gland and evaporatorium only slightly damaged, sac-shaped gland slightly asymmetrical, both ostioles presented.

Odontoscelis fuliginosa, ventral abdominal androconia (Figs 87, 88)

Androconia developed in both sexes, emptying on characteristically sculptured cuticular patches on abdominal venter.

Male (Fig. 87). Large paired and small unpaired androconia developed. Sternum V with one, unpaired, small, median androconium; sternum VI and VII with paired, large, submedian androconium, and small unpaired, median androconium; sternum VIII with one, unpaired, longitudinally oval, median androconium. Female (Fig. 88). Only small, unpaired, median androconia developed. Sternum VI and VII with one, unpaired small androconium; sternum VIII with one unpaired androconium, larger than previous androconia.

CONCLUSIONS AND DISCUSSION

Gland pattern

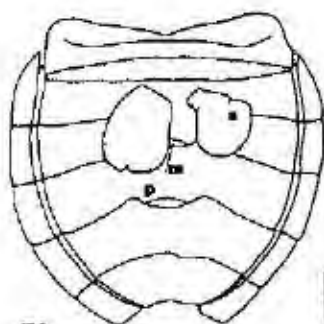
The pattern of the dorso-abdominal scent glands can be characterized in the higher taxa studied as follows (A = adults, Ag = anterior gland, L = larvae, Mg = median gland, Pg = posterior gland).

Plataspidae: L: three unpaired; A: Ag paired, sexually dimorphic, Mg and Pg strongly reduced.

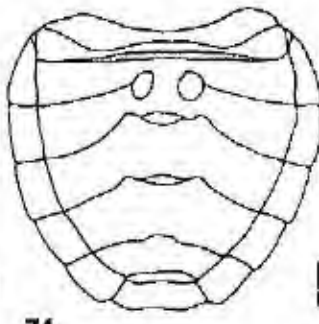
Acanthosomatidae: L: Ag paired, Mg and Pg unpaired; A: Ag paired, Mg and Pg reduced.

Cydnidae:

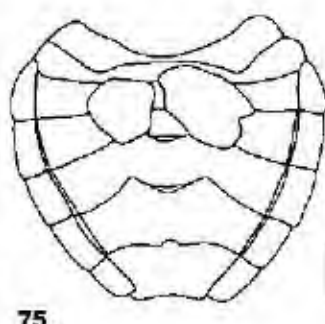
Figs 73-84. Dorso-abdominal scent glands of adults, ventral view. 73, 74 - *Arma custos* (Fabricius), 75, 76 - *Troilus luridus* (Fabricius), 77, 78 - *Rhacognathus punctatus* (Linnaeus), 79, 80 - *Zucrona coerulea* (Linnaeus), 81, 82 - *Eurygaster maura* (Linnaeus), 83, 84 - *Eurygaster testudinaria* (Geoffroy). odd - male, even - female; a - anterior gland, m - median gland, p - posterior gland, dotted area - membranous intersegmental area. Scale - 1 mm.



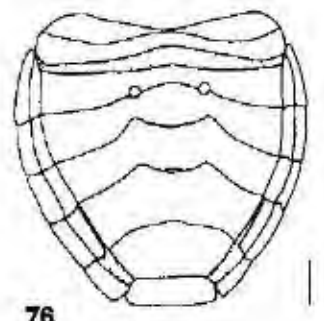
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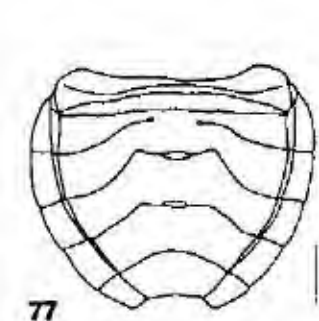
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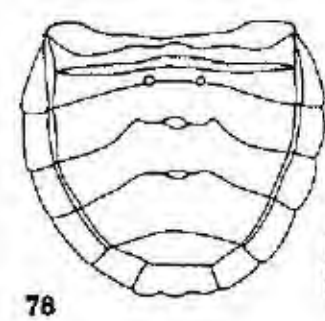
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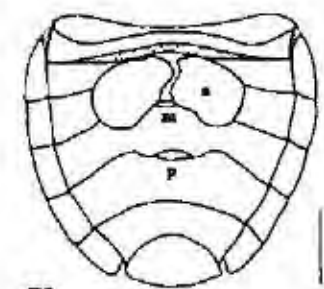
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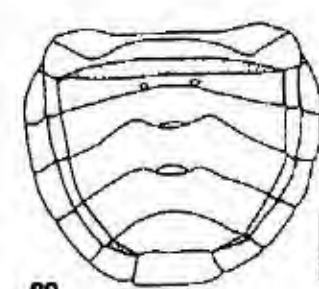
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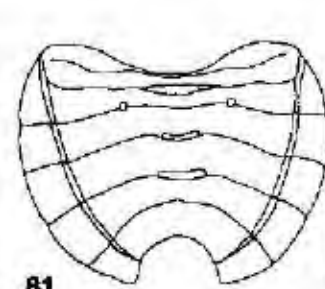
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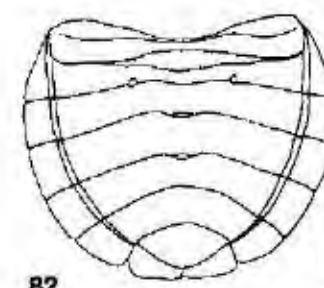
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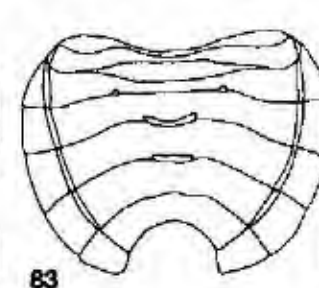
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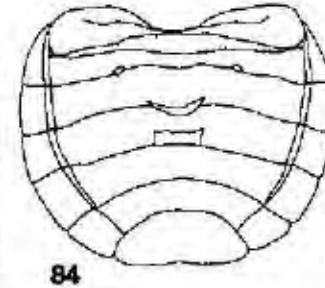
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Cydninae: L: three unpaired; A: Ag paired (*Cydnus aterrimus*), or completely reduced (*Aethus* spp.), Mg and Pg reduced.

Sehirinae: L: Ag paired, Mg and Pg unpaired (*Legnotus limbosus*, *Tritomegas bicolor*), or three unpaired (*T. sexmaculatus*); A: Ag paired, or unpaired (*L. limbosus*, *Tritomegas* spp.), Mg and Pg reduced.

Thyreocorinae: L: not studied; A: Ag unpaired, Mg and Pg completely reduced.

Pentatomidae:

Podopinae: L: Ag paired, Mg and Pg unpaired; A: Ag paired (*Podops inuncta* – sexually dimorphic, Mg and Pg completely reduced), Mg and Pg reduced.

Pentatominae: L: Ag paired, Mg and Pg unpaired; A: Ag paired (slightly sexually dimorphic: larger in male than in female – *Aelia acuminata*; larger in female than in male – *Neottiglossa pusilla*, *Carpocoris fuscispinus*, *Eurydema oleracea*, *E. ornatum*, *Eysarcoris aeneus*, and *Piezodorus lituratus*). Mg and Pg mostly reduced (sac-shaped in *Pentatoma rufipes*, slightly larger in male than in female – *E. oleracea*, slightly larger in female than in male – *P. lituratus*).

Asopinae: L: Ag paired (sexually dimorphic – *Arma custos*, *Zicrona coerulea*), Mg and Pg unpaired; A: Ag paired (sexually dimorphic – *A. custos*, *Troilus luridus*, *Z. coerulea*), Mg and Pg reduced.

Scutelleridae: L: Ag paired, Mg and Pg unpaired; A: Ag paired, Mg and Pg mostly reduced (sac-shaped in *Odontoscotis fuliginosa*).

The paired anterior gland was predominantly developed in adults of the species studied, except of the unpaired gland in *Legnotus limbosus*, *Tritomegas bicolor*, *T. sexmaculatus*, and *Thyreocoris scarabeoides*, or completely reduced in *Aethus flavicornis* and *A. nigrinus*, respectively.

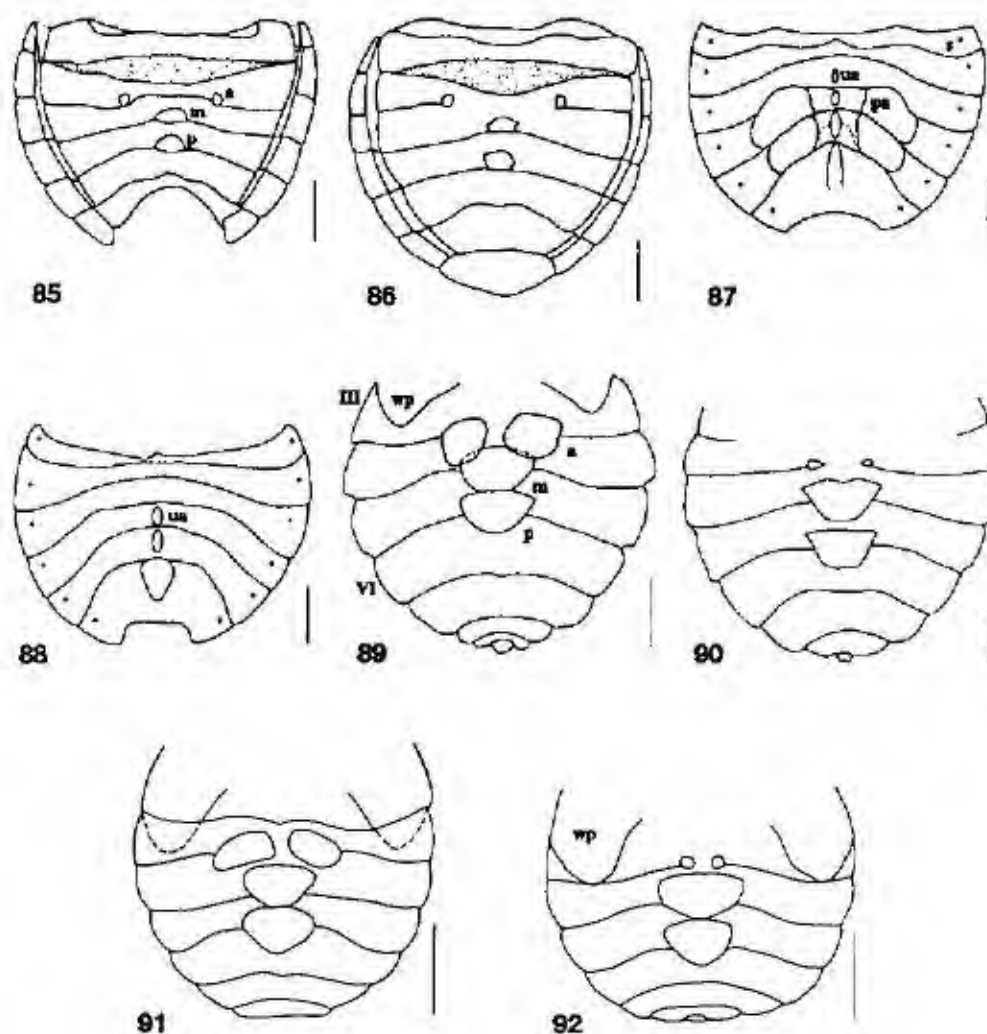
Congeneric species

Two congeneric species of ten genera were studied to estimate the presence of intrageneric variation; Plataspidae: *Coptosoma* spp.; Acanthosomatidae: *Elasmucha* spp.; Cydnidae: Cydninae: *Aethus* spp.; Sehirinae: *Tritomegas* spp.; Pentatomidae: Pentatominae: Aeliini: *Neottiglossa* spp.; Eysarcorini: *Eysarcoris* spp.; Carpocorini: *Carpocoris* spp., *Palomena* spp.; Strachiini: *Eurydema* spp.; and Scutelleridae: *Eurygaster* spp. The obviously specific gland pattern was found only in the genus *Tritomegas*. All the larval glands were unpaired in *T. sexmaculatus*, the anterior gland paired, the median and the posterior glands unpaired in *T. bicolor*; while the adult anterior gland was unpaired in both species.

Persistence in adults, sexual dimorphism

The persistence of the dorso-abdominal glands in adults, at least one of them functional, is probably a common phenomenon in Pentatomoidea. Only three cydnid species, from all the 43 species studied, did not possess the dorso-abdominal glands. The persistence of the adult anterior gland is more common in all Heteroptera (for review see Davidová-Vilšimová & Podoubský in press); many examples of the persistence of at least some of the dorso-abdominal glands in adults, some even sexually dimorphic, were recorded.

The dorso-abdominal gland pattern, found in adults of most the pentatomoidean species studied (anterior paired, median and posterior unpaired) confirms the Polivanova's (1960) hypothesis about the paired origin of the glands. The anterior gland is mostly the only functional dorso-abdominal gland in adults, while size of the larval anterior gland is reduced and its function is probably limited. The pattern is not in agreement with the Polivanova's (1960) hypothesis, that gland reduction proceeds from the posterior to the anterior segments. However, if the adult anterior gland is considered a newly developed structure although occupying the same place as the larval gland, originally with the same or different function (see below), and not a regenerated larval gland functional during larval development, then the findings corroborate the Polivanova's (1960) hypothesis.



Figs 85-92. Figs 85, 86. Dorso-abdominal scent glands of adults, *Odontoscels fuliginosa* (Linnaeus), ventral view. Figs 87, 88. Abdominal venter of adults with androconia, *Odontoscels fuliginosa*, ventral view. Figs 89-92. Dorso-abdominal scent glands of larvae, ventral view. 89, 90 - *Arma custos* (Fabricius), 91, 92 - *Zirona coerulea* (Linnaeus). odd - male, even - female; a - anterior gland, m - median gland, p - posterior gland, pa - paired androconium, s - spiracle, ua - unpaired androconium, wp - wing pad, III, VI - abdominal tergum III, VI, dotted area - membranous intersegmental area. Scale - 1 mm.

The different larval versus adult state of the anterior gland was found in some species. The larvae of both *Coptosoma* species (Plataspidae), and *Aethus flavicornis* and *Cydus aterrimus* (Cydnidae: Cydninae) exhibit the apomorphic gland pattern within Pentatomoidea - all the three glands are unpaired. The adult anterior gland is paired (*C. aterrimus*) (plesiomorphy), paired and sexually dimorphic (*Coptosoma* spp.), or completely reduced (*A. flavicornis*) respectively. The situation supports the idea that the gland is most likely a newly developed adult structure, rather than a structure formed by the cells forming the small, partly reduced larval gland.

The larvae of *Legnotus limbosus* and *Tritomegas bicolor* have paired anterior glands, transformed subsequently into unpaired adult glands. The unpaired adult anterior gland represents a rare state, recognized only in these two species. The adult anterior gland of *Thyreocoris scarabaeoides* (Cydnidae: Thyreocorinae) is described as unpaired. However, the gland is almost completely reduced, and the situation could be generalized for *T. scarabaeoides* and for both *Aethus* species: All the three adult glands are completely or nearly completely reduced, and their remnants are not functional. This conclusion corresponds with Staddon's (in press) results on *T. scarabaeoides* and another cydnin studied, *Geotomus punctulatus* (no ductules found, see below in detail).

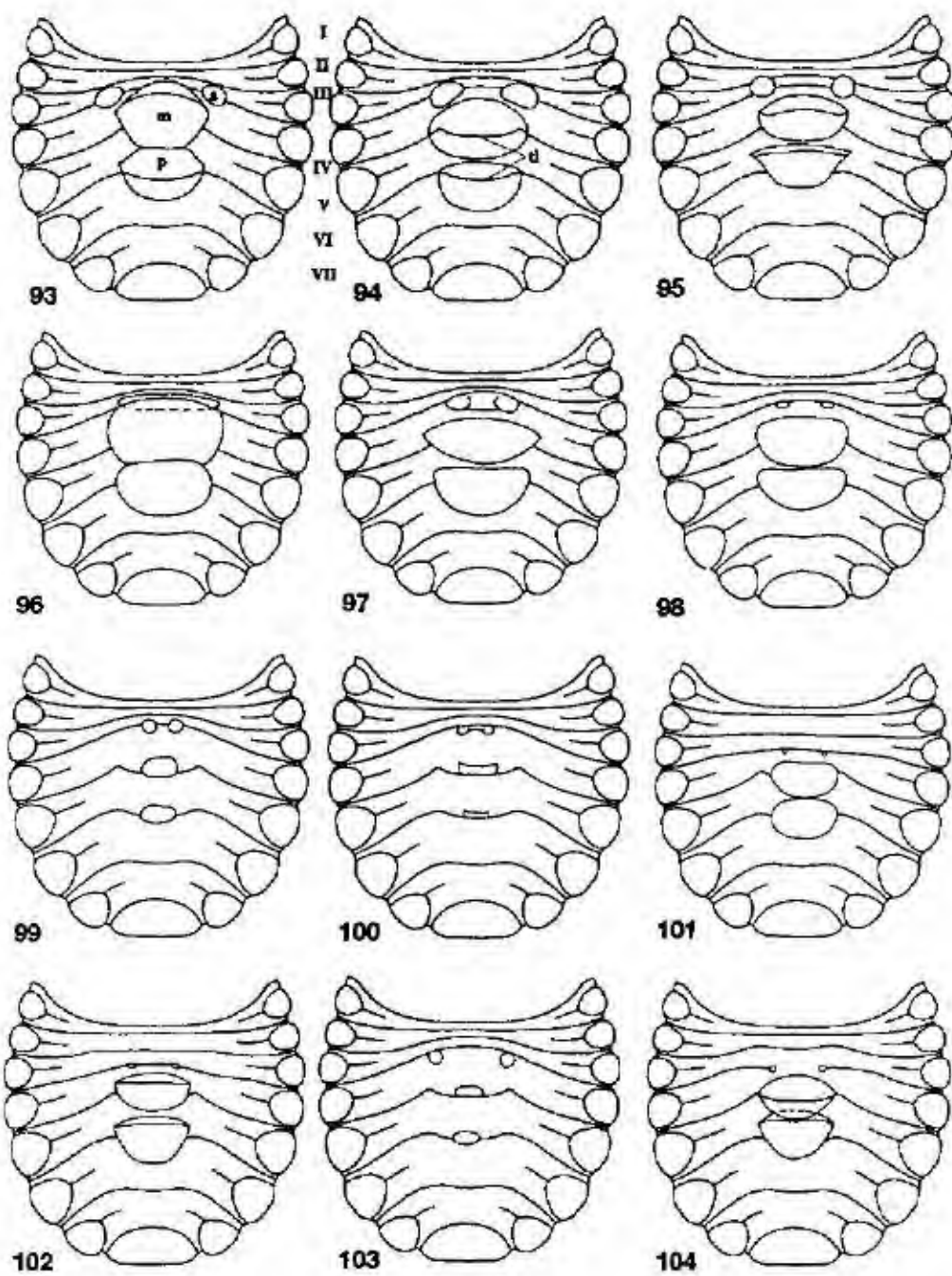
Staddon (in press) mentioned the adult dorso-abdominal glands without ductules recognized in several pentatomoidean representatives. His results fit the present results of morphological study in the following species, *Thyreocoris scarabaeoides* (the anterior gland conspicuously small, the median and the posterior not developed at all), and basically in *Neottiglossa pusilla*, *Eurydema oleracea*, and *Rhacognathus punctatus* (the median and the posterior glands very small). On the contrary, small or even quite large glands were found in several species, in which Staddon (in press) did not record any ductules, *Odontoscels fuliginosa*, *Sciocoris cursitans*, *Aelia acuminata*, *Eysarcoris aenea*, *Dolycoris baccarum*, *Piezodorus lituratus*, *Troilus luridus*, and *Zierona coerulea*. All the other Staddon's (in press) results correspond with the described structural states. Except of *Eurydema maura*, where both the median and the posterior glands are small while Staddon (in press) described significantly more ductules in these glands than in the anterior gland.

Staddon (in press) reported three different patterns of the sexual dimorphism and considered this state as the apomorphy.

1. The anterior gland with a higher number of the ductules in male than in female; only in *Zierona coerulea* (see below in detail).
2. The median and the posterior glands with more ductules in male than in female, *Dolycoris baccarum*, *Piezodorus lituratus*, *Eurydema oleracea*, and *Eurydema dominulus*. The structural gland condition in the two former species does not agree with Staddon's (in press) results. All the glands in both sexes of *D. baccarum* are small, approximately of the same size; the median and the posterior glands are even larger in female than in male of *P. lituratus*. The structural condition found in *E. oleracea* roughly fits Staddon's (in press) result. *E. dominulus* was not studied.
3. The median and the posterior glands with more ductules in female than in male, *Sciocoris cursitans* and *Picromerus bidens*. The structural gland condition is quite different, size of the glands is the same in both sexes of both species.

We can presume, in comparison of our morphological data with Staddon's (in press) histological findings, that size of the gland, or gland remnant, may not correspond with the number of ducted

Figs 93-104 Schemes of larval abdominal dorsum with secret glands, ventral view 93 - *Elasmotethus interstinctus* (Linnaeus), 94 - *Elasmucha fieberi* (Jakovlov), 95 - *Elasmucha ferrugata* (Fabricius), 96 - *Aethus flavicornis* (Fabricius), 97 - *Cydus aterrimus* (Forster), 98 - *Legnotus limbosus* (Costa), 99 - *Tritomegas bicolor* (Linnaeus), 100 - *Tritomegas sexmaculatus* (Rambur), 101 - *Vilpianus galu* (Wolff), 102 - *Graptosoma lineatum* (Linnaeus), 103 - *Ancyrosoma leucogrammes* (Gmelin), 104 - *Sciocoris cursitans* (Fabricius). a - anterior gland, m - median gland, p - posterior gland, tl - transverse line, I - VII - abdominal terga I - VII



secretory units. Thus, it is not possible to distinguish explicitly the functional gland according to single feature.

Possible functionality of the median and the posterior glands is still uncertain in Pentatomoidea. These glands were described as "vestigial glands" by most of serious authors. Two, not so strictly different shapes of the glands are described in the present paper: "Croissant" with a larger remnant of gland tissue than in "horn". The course of reduction from the functional gland through croissant-shaped to horn-shaped gland to completely reduced gland should be supposed. The shape of the glands is uniform within the species, and mostly stable even within a higher taxa. Only in *Acanthosoma haemorrhoidale* a different state is developed in male (horn gland) and in female (croissant gland), a difference which can be interpreted in a scheme of gradual gland reduction. Morphological results corroborate the hypothesis that both the median and the posterior glands of the pentatomoideans are probably not functional. These glands mostly appear as small, empty, membranous sacs.

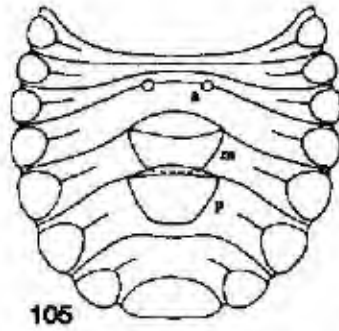
The most uniform adult gland pattern was found in Acanthosomatidae, Scutelleridae, and especially Pentatominae. The anterior gland is always paired (also in larvae), the median and the posterior glands are always unpaired.

The most variable adult gland pattern occurs in Cydnidae and Podopinae. The anterior gland is paired or unpaired, interspecifically variable even in larvae of one genus (*Tritomegas* spp.); the median and the posterior glands are reduced but still distinct in the cydnid subfamily Sehirinae. The anterior gland is paired, small, or not developed at all, the median and the posterior glands are reduced in Cydninae. The anterior gland is strongly reduced, the median and the posterior glands are completely reduced in Thyreocorinae. Slight sexual dimorphism of the paired anterior gland occurs (*Podops inuncta*), or the gland is small to large; the median and the posterior glands are reduced or not developed at all in Podopinae.

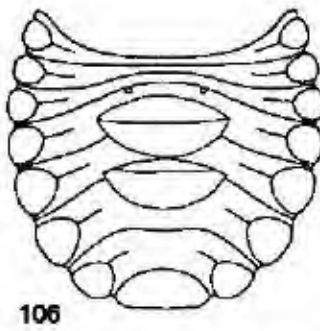
Cydnidae is considered the most primitive pentatomoidean family, Podopinae is the most variable subfamily of Pentatomidae. The gland pattern corresponds apparently with the variety of diverse habitats inhabited by the cydnids and podopines. The variable pattern corresponds also with the way of life of the taxa studied. Complete reduction of all or some of the glands was recorded in the species inhabiting litter, or digging in soil or sand (*Podops inuncta*, *Aethus flavicornis*, *Aethus nigrinus*, *Thyreocoris scarabaeoides*). Reduction of gland(s) could thus be related to the special way of life, preventing dispersion of gland secretion in air, and demanding another way of communication. The slightly larger anterior gland in male than in female was found in *P. inuncta*. Histological and/or biochemical studies are necessary to elucidate the function of the glands.

Conspicuous or slight sexual dimorphism of the adult anterior gland was observed in five phytophagous representatives of Pentatomoidea. Two types of sexual dimorphism were recognized in the species studied, respectively: the anterior gland slightly larger in male than in female, i. e. male dimorphism in *Podops inuncta* and *Aelia acuminata*, and the anterior gland slightly larger in female than in male, i. e. female dimorphism in *Tritomegas bicolor*, *Neottiglossa pusilla*, *Carpocoris fuscispinus*, *Eurydema oleracea*, *E. ornatum*, *Eysarcoris aeneus*, and *Piezodorus lituratus*. Sexual dimorphism in *Eysarcoris* species was described also by Staddon (in press). The structural gland pattern differed between the two *Eysarcoris* species studied. The glands are identical in

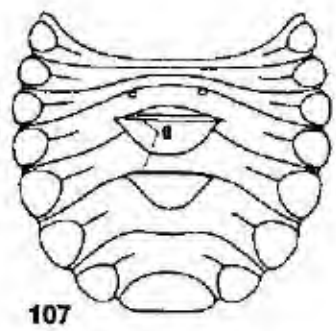
Figs 105–116 Schemes of larval abdominal dorsum with scent glands, ventral view 105 – *Aelia acuminata* (Linnaeus), 106 – *Neottiglossa leporina* (Herrich Schaeffer), 107 – *Eysarcoris fabricii* Kirkaldy, 108 – *Staria lunata* (Hahn), 4th instar, 109 – *Dolycoris barburum* (Linnaeus), 110 – *Holeostethus vernalis* (Wolff), 111 – *Carpocoris fuscispinus* (Boheman), 112 – *Palomena prasina* (Linnaeus), 113 – *Palomena viridissima* (Poda), 114 – *Eurydema oleracea* (Linnaeus), 115 – *Eurydema ornatum* (Linnaeus), 116 – *Rhaphigaster nebulosa* (Poda) a – anterior gland, m – median gland, p – posterior gland, tl – transverse line



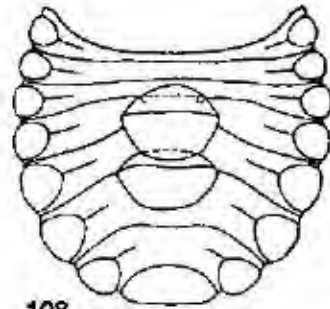
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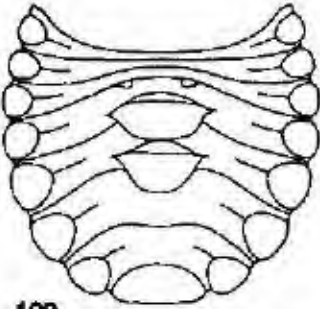
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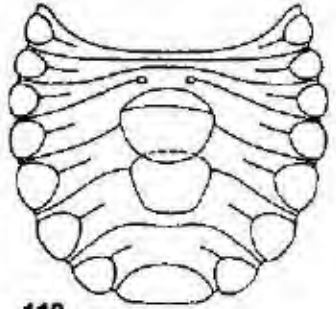
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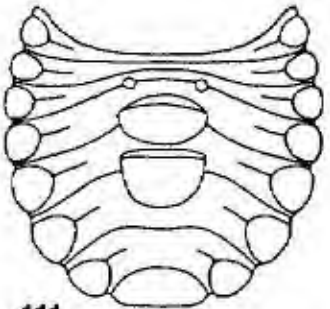
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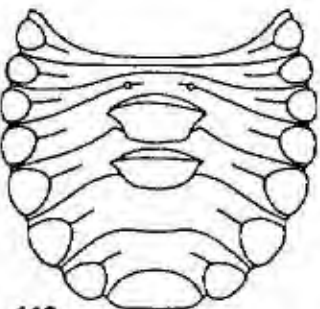
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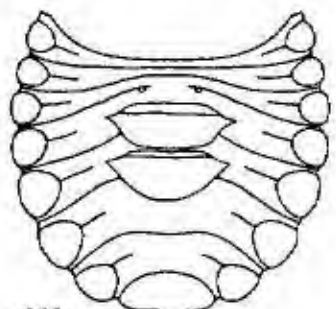
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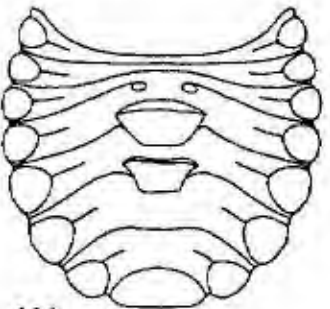
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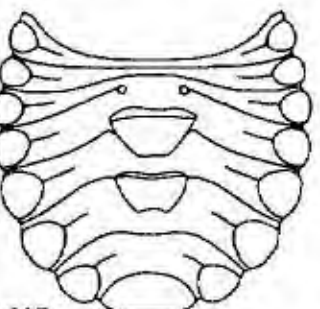
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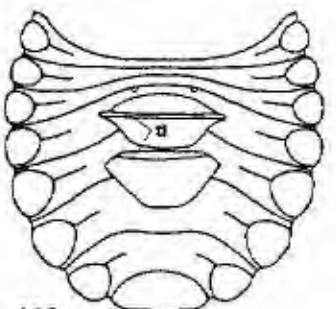
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both sexes of *E. fabricii*, in agreement with findings of Staddon (in press). The female anterior gland is much larger than that in male, the median and the posterior glands are structurally developed in *E. aeneus*. However, Staddon (in press) found more ductules in the male anterior gland than in the female gland, and no ductules in the median and the posterior ones. The female anterior gland is twice as large as the male gland, in both *E. oleracea* and *E. ornatum*, but no sexual dimorphism of the gland was recorded by Staddon (in press) in the former species. However, Staddon described sexual dimorphism in the median and the posterior glands, with more ductules in male than in female, which condition corresponds with the structural state reported in this paper.

A sexually dimorphic adult anterior gland, hypertrophied in the male, was found in numerous asopines (e. g., Dupuis 1959, Aldrich 1995, Aldrich et al. 1986b). The present study confirmed dimorphism in the following Asopinae, *Arma custos* – larvae – new information, adults – the female anterior gland is larger in comparison with other asopines, *Troilus luridus* – only adults, and *Zicrona coerulea* – larvae, adults. The dimorphism was not found in *Picromerus bidens* and *Rhacognathus punctatus*.

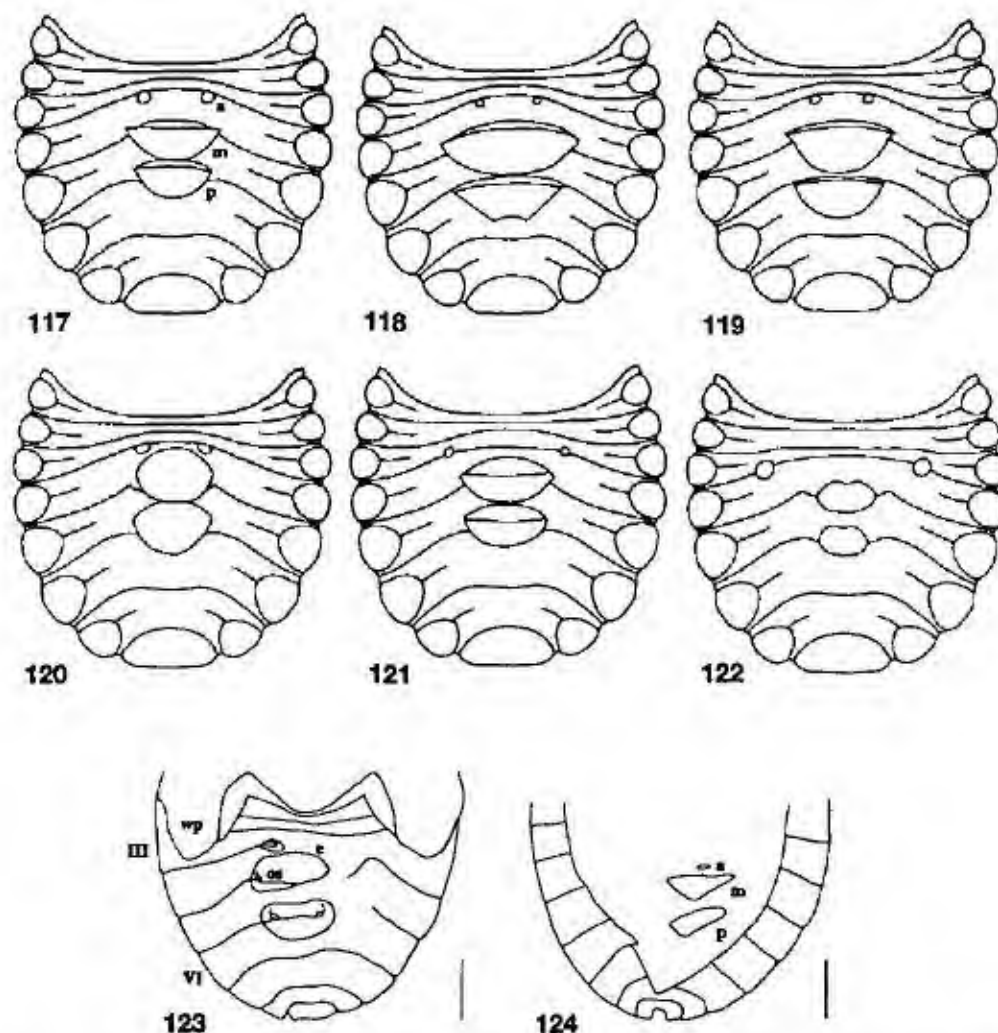
Aldrich et al. (1978) and Aldrich (1988a) explained in detail the development of the gland sexual dimorphism in predaceous Asopinae. However, not all the asopines studied possess the sexually dimorphic anterior gland. We have not found any unambiguous way to explain this situation. Concerning the habitat and the way of life, *Arma custos*, *Troilus luridus* and *Picromerus bidens* all live on trees and/or bushes, however, the former two species have developed sexual dimorphism, contrary to the last one. Similarly, *Rhacognathus punctatus* and *Zicrona coerulea* live on plants or on the ground under vegetation, often in humid habitats. The former species has not developed sexual dimorphism, whereas the latter species possesses a distinctly dimorphic anterior gland. All species are predaceous, without distinct specialization. Therefore, the question remains still open, why only certain predaceous species acquired sexually dimorphic adult dorso-abdominal glands?

The sexually dimorphic anterior glands are developed already in 5th larvae of the two species studied, *Arma custos* (new information) and *Zicrona coerulea* (see Dupuis 1952), while the anterior larval glands are of the same size in both sexes of *Troilus luridus*. The situation as in *T. luridus* similarly exists in *Podisus* species (Aldrich et al. 1978). Two ontogenetic types of the sexually dimorphic glands can be distinguished: larvae with sexual dimorphism – adults with sexual dimorphism, larvae without sexual dimorphism – adults with sexual dimorphism. There is no explanation for the absence of dimorphism in old larvae of certain asopine species with the hypertrophied male anterior gland. Both the larvae and the adults inhabit the same type of biotope and as predators feed on the same kind of prey.

The sexually dimorphic adult glands have been found also in some phytophagous pentatomoid species. The conspicuously hypertrophied anterior gland in male of *Biprorulus bibax* is about 50× larger than the female gland (James & Warren 1989). A sexually dimorphic anterior gland is developed in *Hotea gambiae* (Gough et al. 1985), the gland is larger in the male than in the female. According to illustration, the larval glands are not dimorphic in the 5th larva. A similar state of the anterior gland was described in *Sphaerocoris annulus* (Gough et al. 1986). The male anterior gland is not as extremely hypertrophied in the two latter species (both scutellerids) as that in *B. bibax* but the dimorphism is expressed also by different composition of secretion, evidenced by chemical analysis (e. g., Gough et al. 1985, 1986, Staddon et al. 1987, Aldrich et al. 1990). Another example of an anterior dimorphic gland, demonstrated only structurally, is two *Coptosoma* species (Davidová-Vilimová 1992). The male gland is distinctly larger than the female gland (about 4×) but not as extremely as in *Biprorulus bibax*. Other species with developed male dimorphism, *Podops inuncta* and *Aelia acuminata* were recently found. The size difference, as shown reexamination of several specimens, was small but constant in both the species. All these examples illustrate sexual dimor-

phism, in which the male gland is larger, and therefore assumed to be functional and more important than the female gland.

An example of a quite opposite type of gland sexual dimorphism was reported by Lucchi & Solinas (1990) in *Nezara viridula*, where the female gland was slightly larger than the male gland.



Figs 117-124 Figs 117-122 Schemes of larval abdominal dorsum with scent glands, ventral view 117 - *Piezodorus lituratus* (Fabricius), 118 - *Pentatoma rufipes* (Linnaeus), 119 - *Picromerus bidens* (Linnaeus), 120 - *Troxus luridus* (Fabricius), 121 - *Eurygaster maura* (Linnaeus), 122 - *Odontoscirtus fuliginosa* (Linnaeus) Figs 123, 124. Abdomen of imperfect specimen of 5th larval instar, *Holcostethus vernalis* (Wolff). 123 - dorsal view, 124 - ventral view a - anterior gland, c - evaporative area, m - median gland, os - ostiole, p - posterior gland, wp - wing pad.

Recently, more examples of a female dimorphism have been reported, in *Tritomegas bicolor*, *Neotiglossa pusilla*, *Carpocoris fuscispinus*, *Eurydema oleracea*, *Eurydema ornatum*, *Eysarcoris aeneus*, and *Piezodorus lituratus*. The size difference is small, but constant, similarly to the species with the male dimorphism.

Gough et al. (1985) tried to explain the persistence of the adult dorso-abdominal glands in some Pentatomoidea, but did not mention the development of a sexual dimorphism. Hamilton et al. (1985) explained this phenomenon by a defensive role and possible function as sex pheromone of secretion. Sexual dimorphism can be explained either by importance of chemical defence in males combined with reduction of interference during mating (sexual role), or by greater extent of gland reduction in female than in male, in relation to the larval size. James & Warren (1989) assumed that the male gland in *Biprorulus hibax* may be responsible for the secretion of a pheromone attractive to conspecifics, to inform them about food resources. This explanation is very similar to that concerning asopine dimorphism. It seems logical to assume the same function for the male enlarged gland throughout Pentatomoidea. However, the problem still needs more detailed studies, including behavioral, because the phytophagous pentatomoideans with a male dimorphism, as found in the present study, do not express any specific feature, explaining the need by some but not others of a special chemical communication pathway. The question of the persistence of the female dimorphism, with the anterior gland larger than in the male, remains still unresolved. We might assume the greater need for defence by the female, and therefore expect increased secretion of the gland but, similarly as for the male dimorphism, no specific ethological or ecological feature unites those species showing the female larger gland.

Other biochemical and histological studies is common for understand the function of the sexually dimorphic glands. The number of ductules recognized in the structurally dimorphic glands (Staddon in press), nevertheless, corresponds with structural data in only some species, i. e. *Aelia acuminata*, *Tritomegas bicolor*, *Neotiglossa pusilla*, and *Eurydema oleracea*, and mostly only approximately.

Several our results are quite different from published data. Davidová-Vilimová (1992) described incorrectly the anterior paired gland with unpaired ostiole in the adults of two *Coptosoma* species (Plataspidae). The pattern with anterior paired gland with paired ostioles was confirmed in the present study. The anterior gland of *Elasmotethus interstinctus* was described as the largest one among European Acanthosomatidae (Staddon 1990); our results do not support this finding. The anterior gland of *Elasmucha fieberi* is structurally the relatively largest gland, in relation to the body size. Generally, the anterior glands of acanthosomatids are small, their varied size is related to the functional state (empty or full). Such a dependence is obvious especially in small, not hypertrophied glands. The sexually dimorphic adult anterior gland, with the conspicuously hypertrophied gland in male, was found in three asopine species (see above). We have not observed the tergal sutures with sexually dimorphic pattern, recorded by Aldrich et al. (1984) in *Podisus maculiventris*. The development of these sutures, associated with the large and functional anterior gland, especially in the male, does not probably represent a feature common for all the species with the hypertrophied glands. A small but distinct adult anterior gland is developed in the pentatomids, *Carpocoris pudicus*, *Dolycoris baccarum* and *Raphigaster nebulosa*, in which Boselli (1932) did not reported either glands or ostioles.

Secretion in larval exuviae

Exuviae of *Elasmucha ferrugata* (Acanthosomatidae) were studied after moulting of the 5th larva in the adult. The anterior gland was small and empty, the median and posterior gland sacs were large, of the same size as in the live 5th instar, and full of gland secretion of characteristic smell. This

situation corroborates Aldrich's (1988 a, 1995) conclusion, that leaving of gland secretion in the larval exuviae is common for Pentatomoidea, and probably for most Heteroptera.

Androconia

Carayon (1984) and Knight et al. (1985) recorded androconia only in males of Scutelleridae. We have described patches with androconial glands in both sexes in *Odontoscelsis fuliginosa*. The exact pattern of male androconial patches is described and illustrated for the first time; while a higher number and larger patches are developed in the male, only three small patches are apparent in the female. The patches are of the same structure in both sexes. The androconia are very probably developed in both sexes of the scutellerids. However, Carayon (1984) proposed their specific function as the male sexual glands. The function of androconial secretion is either quite different than proposed, or it is different in male and female, or secretion has more functions.

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We would like to dedicate our study to Brian W. Staddon (Cardiff, United Kingdom), our good friend, who has contributed a lot to the knowledge of the heteropteran glands. We very much appreciate particularly his permission to use data from a MS in press.

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BOOKREVIEW

GORDON D. G. *The Eat-A-Bug Cookbook. 33 ways to cook grasshoppers, ants, water bugs, spiders, centipedes, and their kin*. Berkeley, California: Ten Speed Press, 1998, XXVI + 102 pages. Format 23.7 × 18.7 cm. Price 12.95 USD.

In Moravia a Professor at Mendel University in Brno enjoys eating not only all kind of insects, but spiders and other assorted arthropods. When most of us hear about people eating insects we often feel repugnance. Is this fair? How many insects do we eat in our everyday lives? For instance, in spring, how many unhappy aphids are eaten with the lettuce in a salad? Careful housekeepers wash out the majority of them but many rest hidden in folds of leaves and are ingested as tasty extra ingredients. How many partial insects do we ingest with flour, bread, etc.? The American Food and Drug Administration is aware of insect contamination of food and publishes a list of maximum permissible levels of insect infestation or damage, that is, a maximum number of insect adults, eggs, immature stages, droppings, or fragments with which food can be sold. Just about every food imaginable is on this list!

The eggs of various intestinal helminths, among them eggs of thorny-headed worms (screw worms), have been found in the desiccated faeces (coprolites) of our cave-dwelling prehistoric ancestors. As these parasites use insects as intermediate hosts it is clear that our ancestors had to be infected by them by eating insects. What of our more recent ancestors? The ancient Greeks were known to be avid insect-eaters. Aristotle in his *Historia animalium* wrote that "the larva of the cicada on attaining full size in the ground becomes a nymph then it tastes best, before the husk is broken". *Cossus*, a grub or caterpillar of uncertain identity, was considered as a delicacy in Rome when reared on a flour-based diet. In ancient Africa, plagues of locusts caused little hardship. In the absence of their normal food plants, people of the African bush readily ate the infesting insects.

Bug-eating, also known as *entomophagy* or *arthropodophagy*, still exists in modern times, even if somewhat geographically restricted. In parts of Africa locusts are customarily boiled, cooled, dried, cleaned, and salted. Their legs are ground into flour and cooked with salt and peanut butter. In other parts grubs and caterpillars are highly regarded foods, in Thailand a giant water bug can be found for sale in street markets with canned silkworm larvae and pupae being available in Japanese supermarkets. This may indicate of an increase in entomophagy on a wider scale.

Those would like to try eating insects and other arthropods may now have the opportunity to do so. A cookbook based on preparing insects and other arthropods for consumption was published last year. The introductory chapters, along with other relevant information, concern the benefits of bug-eating (nutritional value of bugs), the seasonal availability of edible arthropods, and advice on the best beverages for accompanying bug-eating. One connoisseur recommends drinking champagne as "there's nothing better than some bubbly to wash bugs down". The body of the book consists of recipes presented in the classical way with all ingredients, quantities needed, and detailed descriptions on how to prepare a meal, whether that be steaming, boiling, sautéing, stir-frying, deep-frying, dry-roasting or grilling your chosen arthropod. To give a further insight into this book, we can list some of the dishes by name. We can prepare for our ourselves, family and friends, such dishes as *Bugs in a Rug*, *St John's Bread* (from locusts), *Three Bee Salad*, *Ants in Pants*, *Cocroach a la King*, *Fried Green Tomato Hornworms*, *Giant Water Bug on Watercress*, *Scorpion Scallopine*, *Ample Drummstick* (from centipedes), *Baked Bird-Eating Spider* and as a dessert *Chocolate Cricket Tortie*. The book is attractively illustrated and contains full-colour inserts demonstrating how results of the cooking should look. It is a well-presented book, and can be recommended, at minimum, as a curiosity.

Josef Chalupský

***Stysiana*, a new genus and four new species of Pentatomini
(Heteroptera: Pentatomidae) of the Neotropical region**

Jocélia GRAZIA¹⁾, José Antônio Marin FERNANDES²⁾ & Cristiano Feldens SCHWERTNER³⁾

Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Av. Paulo Gama s/n,
90046900, Porto Alegre, Rio Grande do Sul, Brazil

¹⁾ email: jocelia@vortex.ufrgs.br; ²⁾ email: josefern@conex.com.br; ³⁾ email: bobschwe@vortex.ufrgs.br

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Abstract *Stysiana* gen. n. is described to include four new species, *S. pardidens* sp. n., type species, from Guyana, Colombia, Brazil and Peru, *S. acarinatus* sp. n. from Paraguay and Argentina, *S. tropicalis* sp. n. from Trinidad, Suriname and Brazil, and *S. meridionalis* sp. n. from southern Brazil and Argentina. *Stysiana* gen. n., with its species, are keyed with other three correlated genera, *Amauromelpia* Fernandes et Grazia, 1998, *Hypatropis* Bergroth, 1891 and *Luridocimex* Grazia, Fernandes et Schwertner, 1998.

Taxonomy, morphology of genitalia, new species, key, Pentatomidae, *Stysiana* gen. n., Neotropical region

INTRODUCTION

Stysiana gen. n. belongs to a group of genera with similar facies which includes *Hypatropis* recently revised by Fernandes & Grazia (1996), *Amauromelpia*, and *Luridocimex*. By the absence of a tubercle on third urosternite, these four genera fit with Section 1 of Pentatomini (Rolston & McDonald 1984). Four new species are described: *Stysiana pardidens* sp. n. from northern part of South America, *S. acarinatus* sp. n. and *S. meridionalis* sp. n. from southern part of South America and *S. tropicalis* sp. n. with a central distribution in the Neotropical region, ranging from Trinidad to southeast of Brazil.

MATERIAL AND METHODS

The specimens studied belong to the following collections: American Museum of Natural History, New York, N. Y., USA (AMNH); Departamento de Zoologia, Universidade Federal do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil (UFRG); Entomological Collection, Department of Entomology, National Museum of Natural History, Washington, District of Columbia, USA (NMNH); Facultad de Ciencias Naturales y Museo, Universidad Nacional de La Plata, La Plata, Argentina (MULP); Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina (MACN); Museu de Ciências Naturais, Fundação Zoológica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul, Brazil (MCNZ); Museu de Zoologia, Universidade de São Paulo, São Paulo, SP, Brazil (MZSP); Rijksmuseum Natural History, Leiden, Netherland (RMNH); The Natural History Museum, London, England (BMNH).

Measurements are given in millimeters. The terminology of Dupuis (1970) was adopted for the structure of the genitalia. The only male of *S. meridionalis*, was not dissected, then description and illustrations of phallus were not done.

Portions before and after vesicular area were omitted in the illustrations of females' ductus receptaculi due to it's extremely long extension.

Stysiana gen. n.

TYPE SPECIES. *Stysiana pardidens* sp. n.

DESCRIPTION. Medium size. Elliptical-shaped body; ventral surface moderately convex, dorsal surface nearly flattened. Pale yellow to castaneous. Dorsal surface densely and uniformly punctured with ferrugineous punctures. Abdominal ventral surface with more concentrated and slightly small punctures.

Jugae longer than tylus, contiguous or not before tylus. Antenniferous tubercles with a lateral rhomboid spine. Antennal segment I not attaining apex of head; I the shortest; III and V subequal in length longer than IV, this longer than II. Head in profile with jugae in a higher level than tylus. Bucculae with a small anterior tooth, rectilinear in profile, subtruncated at base of head. Rostral segment I as long as bucculae and obscured by them in profile. Rostral segment II subequal to III and IV together. Ventral surface of head with punctures almost uniformly distributed, sometimes concentrated at bucculae and adjacent areas.

Pronotum trapezoidal. Anterior angles distinctly toothed. Anterolateral margins moderately convex; posterolateral margins sinuous. Posterior margin slightly concave. Humeral angles not protruding. Concolorous cicatrices, delimited by punctures, and with few punctures at middle. A narrow row of white hairs along prosternum. Mesosternum carinate or not, recovered by white hairs. Metasternum plane or concave. Each ostiolar rugae in a short tongue developed through 1/6 metapleurial width. Evaporative area dull and sculptured. Basal angles of scutellum foveated, apex rounded surpassing middle of connexival segment V. Posterior angle of corium acute reaching at least base of connexival segment VI. Apex of radial vein with a small pale yellow callus. Corium almost uniformly punctured, with two impunctured narrow strips, each one along radial vein. Hemelytral membrane hyaline and infuscated, with seven brown veins. Tibiae dorsally sulcated. Femora and tibiae with piceous dots at base of hairs. Tarsi immaculated.

Well-exposed connexivum with concolorous punctures sometimes bordered dark-castaneously. Posterolateral angles of connexivum almost rectilinear. A pair of trichobothrium at midway the spiracles and posterior border of abdominal segments; each trichobothrium separated by the imaginary longitudinal line tangential to spiracles. Subcaloused pale-yellow little spots, inner to spiracles, not punctured. Abdominal lateral margins finely, lighter and less punctured. Abdominal ventral disc almost uniformly punctured, median longitudinal strip less punctured; sometimes darker and densely punctured along spiracles.

Male pygophore (Figs 5–20) quadrangular, globose, external opening dorso-posteriorly. Posterolateral angles rounded. Dorsal rim (dr) posteriorly projected covering pygophoral cup at base, or not; middle third shallowly concave. Ventral rim (vr) forming two layers; the superior one (sl) expanded in 1+1 arms (sa) dorsally-directed, each one parallel segment X, inner angle not projected toward longitudinal plane. Inferior layer (il) carinated, with 1+1 toothlike projections (tp); carina evanescent between them. Surface of ventral rim, between layers, irregularly concave, covered with hairs. Segment X (x) cylindric, with a transversal carina (cr) near middle length, apex roundly expanded. Parameres absent. Phallus (Figs 21–29) almost as long as wide, dorsoventrally flattened. Articulatory apparatus with simple basal plates; dorsal connectives (dc) and processus capitati (pca) well-developed. Phallotheca (ph) broadly opened posteriorly, with one ventromedian process, processus phallothecae (pph), in 1+1 clavate arms, subparallel, laterally depressed dorsally curved. Posterolateral angles of phallotheca developed or not. Conjunctiva (cj) complex with two sclerotized processes: one ventral, processus conjunctivae 1 (prcj1), in 1+1 divergent, strongly sclerotized cylindrical arms, with apex dorsally-curved, longer than processus phallothecae; the other dorsolateral, processus conjunctivae 2 (prcj2), in 1+1 stout structures, dorsally curved at

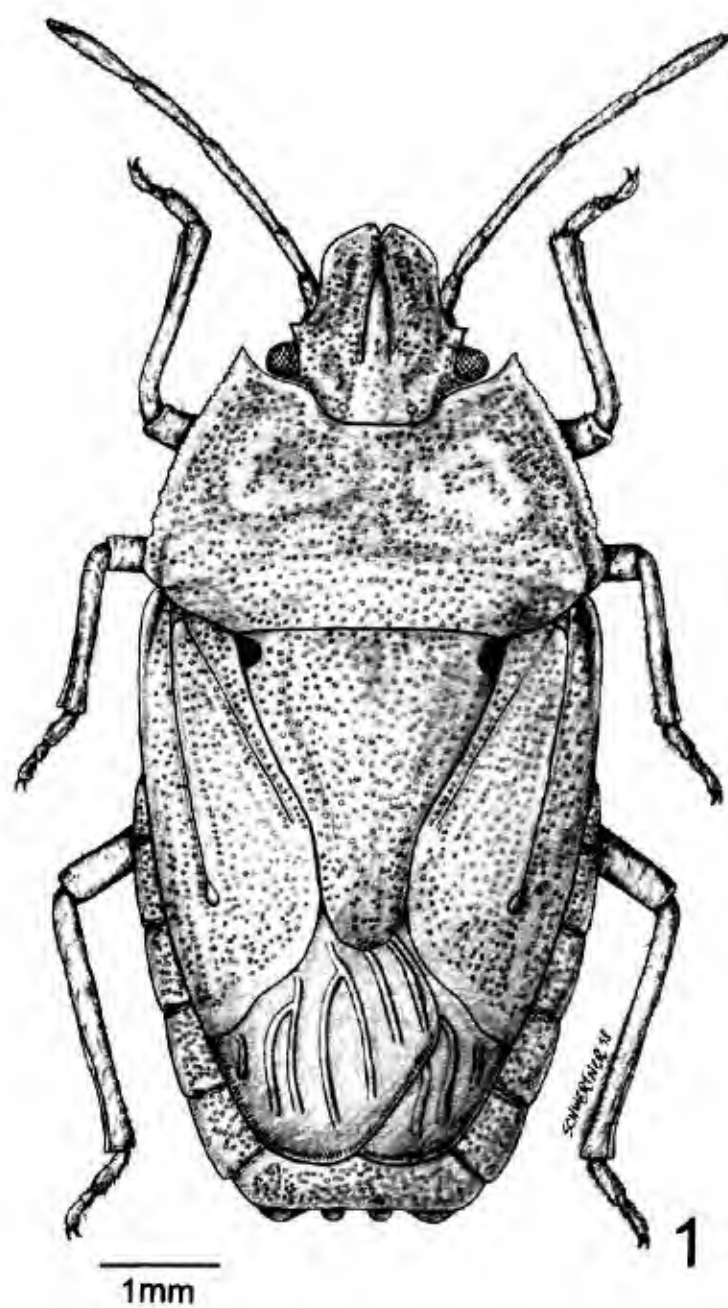
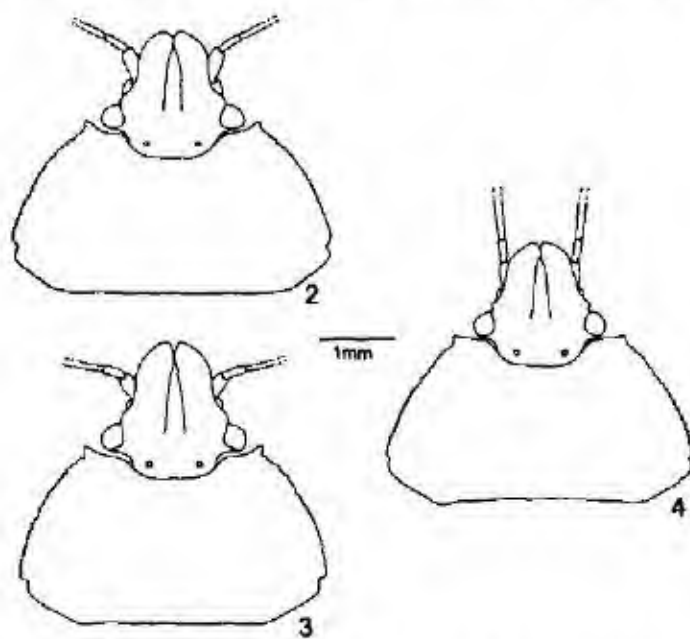


Fig. 1. Habitus. *Stysiana pardidens* sp. n., female.

apex; a small, sclerotized tumescence (tu) laterally to processus conjunctivae 2. Vesica (v) with a dorsal shield-like processus, processus vesicae (prv), expanded in two flaps ventrally; membranous side in a ventral shapeless collar. Ductus seminis distalis (dsd) extremely long, helicoidal and very delicate, usually not preserved after dissection.

Female. (Figs 30–37) Surface of gonocoxites 8 (gc8) convex; posterior border subrectilinear; posterolateral angles truncate; mesial borders parallel in almost all extension. Spiracles absent in laterotergites 8 (la8), posterior border slightly concave. The fused gonocoxites 9 (gc9) trapezoidal, posterolaterally tumid, anterolaterally expanded in 1+1 curved arms. Laterotergites 9 (la9) long, with rounded apices. Gonocoxites 8 and laterotergites 8 densely punctured; laterotergites 9 finely punctured; gonocoxites 9 and segment X less punctured. Secondary thickenings (st) of gonapophyses 9 (g9) partially hiding chitinellipson (ch). Thickening of vaginal intima (tvi) conical. Ductus receptaculi (dur) extremely long, wound before and after vesicular area (va). Pars intermedialis (pi) with a narrow sclerotized ring at base. Annular crests (aac, pac) convergent, or anterior annular crest (aac) turned toward vesicular area of ductus receptaculi. Capsula seminalis (cs) shorter than pars intermedialis; tooth-like processes absent.

DIFFERENTIAL DIAGNOSIS. The new genus is related to *Hypatropis*, *Amauromelpia* and *Luridocimex*; they share the following characters: head in profile with jugae in a higher level than tylus, and parameres absent. Also, in the structure of female internal genitalia (except in *Luridocimex*, not dissected in Grazia et al. 1998), they share a ductus receptaculi extremely long, and well-developed secondary thickenings of gonapophyses 9. With *Luridocimex*, *Stysiana* gen. n. shares the depressed dorsal surface of the body, the convex anterolateral margins of pronotum, segment X ampliate at apex, and tumid areas of gonocoxites 9; they could be distinguished by the number of



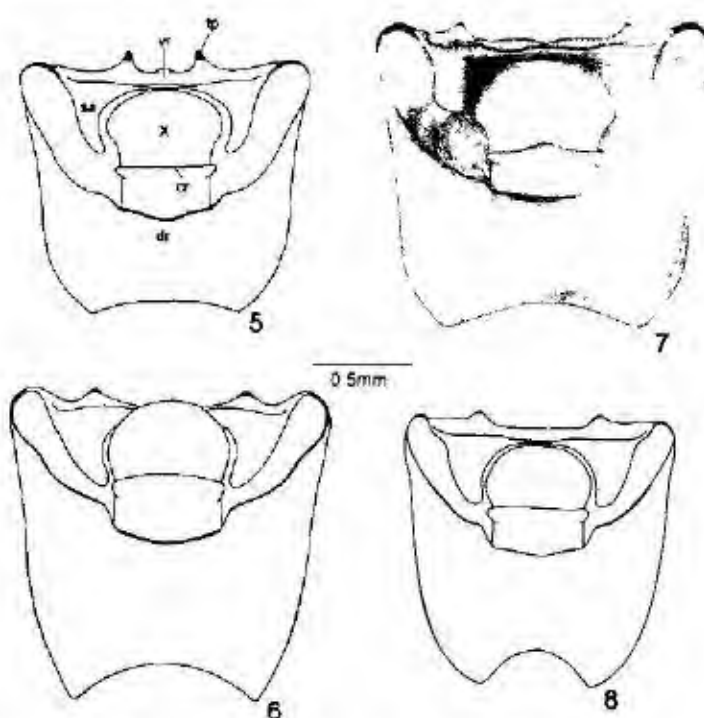
Figs 2–4 Head and pronotum, dorsal view 2 – *Styxiana acarinatis* sp. n., 3 – *S. meridionalis* sp. n., 4 – *S. tropicalis* sp. n.

toothlike projections at inferior layer of ventral rim of pygophore, and by the proportional length of the second rostral segment. The strongly sclerotized processus conjunctivae 1 in *Stysiana* gen. n. are similar to *Amauromelpia*, which, beside other characters, distinguished them from *Hypatropis*. DISTRIBUTION. Argentina (Buenos Aires, Corrientes, Misiones). Brazil (Rondônia, Maranhão, Minas Gerais, Espírito Santo, Santa Catarina). Colombia, Guyana, Paraguay (Assuncion), Peru, Suriname, Trinidad.

ETYMOLOGY. Named in honor to Prof. Pavel Štys for his great contribution to the knowledge of the hemipterous insects; feminine in gender.

Key to genera of *Hypatropis* genera group and to species of *Stysiana* gen. n.

- 1 Antero-lateral margins of pronotum subrectilinear or concave, head and pronotum declivent. 2
- 1' Antero-lateral margins of pronotum convex (Figs 1–4), head and pronotum not declivent, dorsal surface uniformly flat 3
- 2 Segment X without transversal carina, phallus with very sclerotized ventral processes of conjunctiva *Amauromelpia* Fernandes et Grazia, 1998
- 2' Segment X with a transversal carina, phallus with less sclerotized ventral processes of conjunctiva. *Hypatropis* Bergroth, 1891
- 3 Second rostral segment shorter than III and IV together; in male, inferior layer of ventral rim of pygophore with one median tooth-like projection *Luridocimex* Grazia, Fernandes et Schwertner, 1998



Figs 5–8 Pygophores, dorsal view. 5 – *S. acuminatus* sp. n., 6 – *S. meridionalis* sp. n., 7 – *S. pardidens* sp. n., 8 – *S. tropicalis* sp. n. (cr = carina, dr = dorsal rim, sa = superior arms, tp = tooth-like projections of inferior layer of ventral rim, vr = ventral rim, X = tenth abdominal segment).

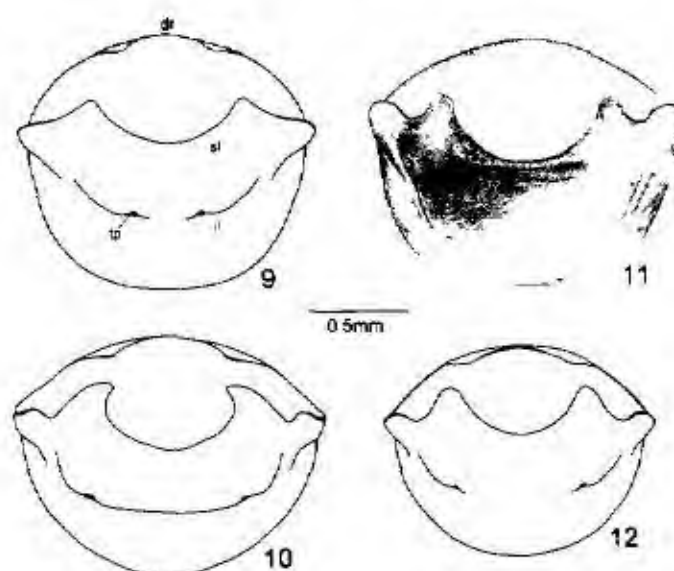
- 3* Second rostral segment almost as long as III and IV together, in male, inferior layer of ventral rim of pygophore with 1+1 tooth-like projections (Figs 5, 9, 13, 17) (*Stysiana* gen. n.) 4
 4 Mesosternum carinate 5
 4' Mesosternum not carinate *S. acarinatus* sp. n. 6
 5 Mesosternal carina developed, in a keel-like structure
 5' Mesosternal carina reduced, truncate at apex *S. tropicalis* sp. n.
 6 Tooth of antero-lateral margins of pronotum long and forward directed (Fig. 1) *S. parddens* sp. n.
 6' Tooth of antero-lateral margins of pronotum short and laterally directed (Fig. 3) *S. meridionalis* sp. n.

***Stysiana acarinatus* sp. n.**
 (Figs 2, 5, 9, 13, 17, 21, 24, 27, 30, 34)

TYPE MATERIAL: Holotype male - PARAGUAY, Assuncion, 15 I 1983, E. G. Riley coll., L. H. Rolston Collection (NMNH). Paratypes: 2 males and 1 female, same data as holotype, 1 female, ARGENTINA, Misiones, Loreto, 9 1935, Berg. coll. (MULP), 1 male, ibidem, (UFRG), 1 male Loreto, 10 1935 (MULP), 2 females, Corrientes, 1 1921, coll. De Carlo (MULP).

DESCRIPTION: Jugae contiguous before tylus, lateral margins of jugae sinuous. Anterolateral angles of pronotum with a short, laterally directed tooth (Fig. 2). Mesosternum not carinate. Metasternum plane.

Male. Body length 7.63 (6.81-8.45), abdominal width 4.03 (3.61-4.26), head length 1.62 (1.48-1.64), length before eyes 0.89 (0.82-0.90), width through eyes 1.79 (1.64-1.89), width before eyes 0.92 (0.82-0.98), width between eyes 1.21 (1.15-1.31), distance ocellum-eye 0.35, length of antennal segments: I 0.39 (0.33-0.41), II 0.30 (0.25-0.33), III 0.80 (0.74-0.90), IV 0.67 (0.57-0.74), V 0.85



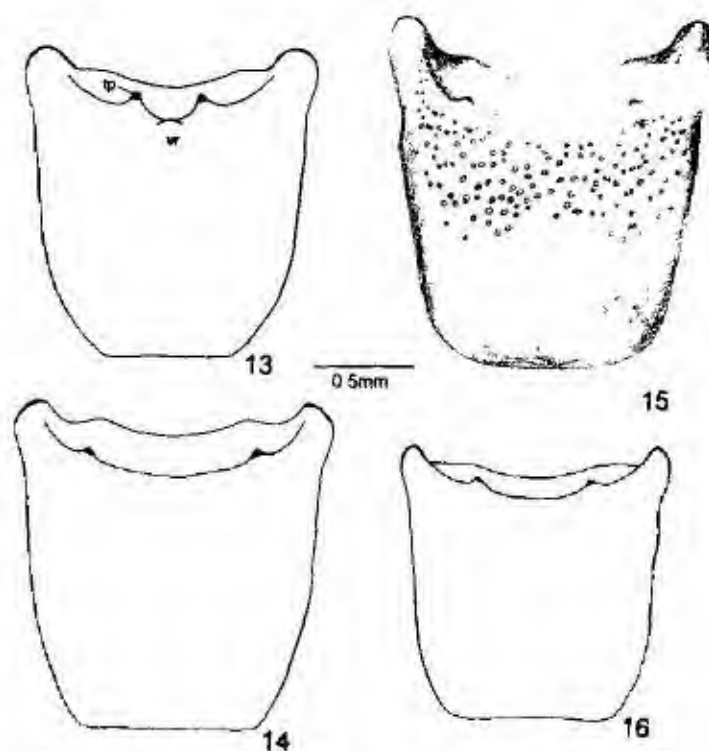
Figs 9-12. Pygophores, posterior view: 9 - *S. acarinatus* sp. n., 10 - *S. meridionalis* sp. n., 11 - *S. parddens* sp. n., 12 - *S. tropicalis* sp. n. (dr = dorsal rim, sl = superior layer of ventral rim, tp = tooth-like projections of inferior layer of ventral rim)

(0.82–0.90); scutellar length 2.67 (2.30–2.87), scutellar width 2.39 (2.05–2.54); pronotal length 1.67 (1.48–1.80), pronotal width 3.87 (3.44–4.18); corium length 3.48 (3.12–3.69).

Pygophore: postero-lateral angles less developed; dorsal rim less projected. Superior layer of ventral rim of pygophore expanded in digitiform arms. Tooth-like projections of inferior layer of ventral rim closer to each other than in the other species. Ventral rim tumid between tooth-like projections (Figs 5, 9, 13, 17). Posterolateral angles of phallotheca not developed. Processus phallothecae slightly curved dorsad. Processus conjunctivae 2 digitiform, cylindrical (Figs 21, 24, 27).

Female. Body length 8.47 (8.28–8.69); abdominal width 4.45 (4.26–4.67); head length 1.70 (1.64–1.72); length before eyes 0.92 (0.90–0.98); width through eyes 1.82 (1.80–1.89); width before eyes 0.96 (0.90–0.98); width between eyes 1.29 (1.23–1.31); distance ocellum-eye 0.33; length of antennal segments: I 0.41; II 0.33; III 0.80 (0.74–0.82); IV 0.70 (0.66–0.74); V 0.84 (0.82–0.90); scutellar length 2.87 (2.79–2.95), scutellar width 2.50 (2.38–2.62); pronotal length 1.76 (1.72–1.80), pronotal width 4.06 (3.94–4.18); corium length 3.77 (3.69–3.85).

Tumescences of gonocoxites 9 forming short digitiform processes (Fig. 30). Secondary thickenings of gonapophyses 9 with claviform projections. Annular crests convergent. Capsula seminalis globose-ovoid (Fig. 34).



Figs 13–16. Pygophores, ventral view, 13 – *S. acarinus* sp. n., 14 – *S. meridionalis* sp. n., 15 – *S. pardidens* sp. n., 16 – *S. tropicalis* sp. n. (tp = tooth-like projections of superior layer of ventral rim).

DISTRIBUTION. Argentina (Corrientes, Misiones), Paraguay (Assuncion).

ETYMOLOGY. Name allusive to the absence of a carena on mesosternum.

DIFFERENTIAL DIAGNOSIS. For differential diagnosis see key above.

Stysiana meridionalis sp. n.

(Figs 3, 6, 10, 14, 18, 31, 35)

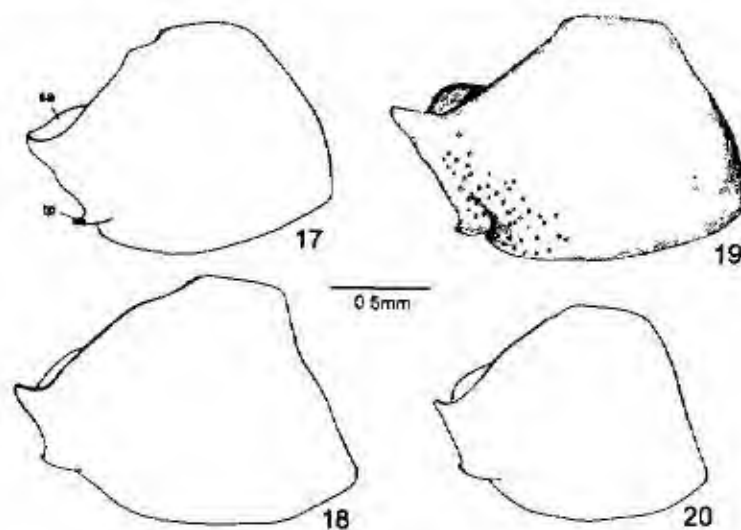
TYPE MATERIAL. Holotype: male - BRAZIL, Santa Catarina, Morro das Pedras, 22.I.1957, Pe. Buck leg. (MCNZ). Paratypes: 2 females, ARGENTINA, Buenos Aires, J. B. Daguerre coll. (MACN, UFRG).

DESCRIPTION. Jugae contiguous before tylus, divergent at apex; lateral margins clearly toothed just before eyes. Antero-lateral angles of pronotum with a short, laterally directed tooth (Fig. 3). Anterior third of mesosternum with a well developed carina, in a keel-like structure, evanescent backward. Metasternum damaged.

Male. Body length 8.20; abdominal width 3.93; head length 1.88; length before eyes 1.14; width through eyes 1.88; width before eyes 0.98; width between eyes 1.31; distance ocellum-eye 0.24; length of antennal segments I 0.41; II 0.32; III 0.98; IV 0.73; V 0.98; scutellar length 2.95, scutellar width 2.29; pronotal length 1.80, pronotal width 3.28; corium length 3.85.

Pygophore: postero-lateral angles developed; dorsal rim well projected. Superior layer of ventral rim of pygophore expanded in subtriangular arms. Tooth-like projections of inferior layer of ventral rim far apart from each other (Figs 6, 10, 14, 18).

Female. Body length 9.39 (9.27-9.51); abdominal width 4.39 (4.26-4.51); head length 1.85 (1.80-1.89); length before eyes 1.11 (1.07-1.15); width through eyes 1.97; width before eyes 1.07; width between eyes 1.31; distance ocellum-eye 0.33; length of antennal segments I 0.49; II 0.33; III 0.90; IV 0.74; V 0.94 (0.90-0.98); scutellar length 3.12 (3.03-3.20), scutellar width 2.58 (2.54-2.62); pronotal length 1.93 (1.89-1.97), pronotal width 4.10 (4.02-4.18); corium length 4.26.



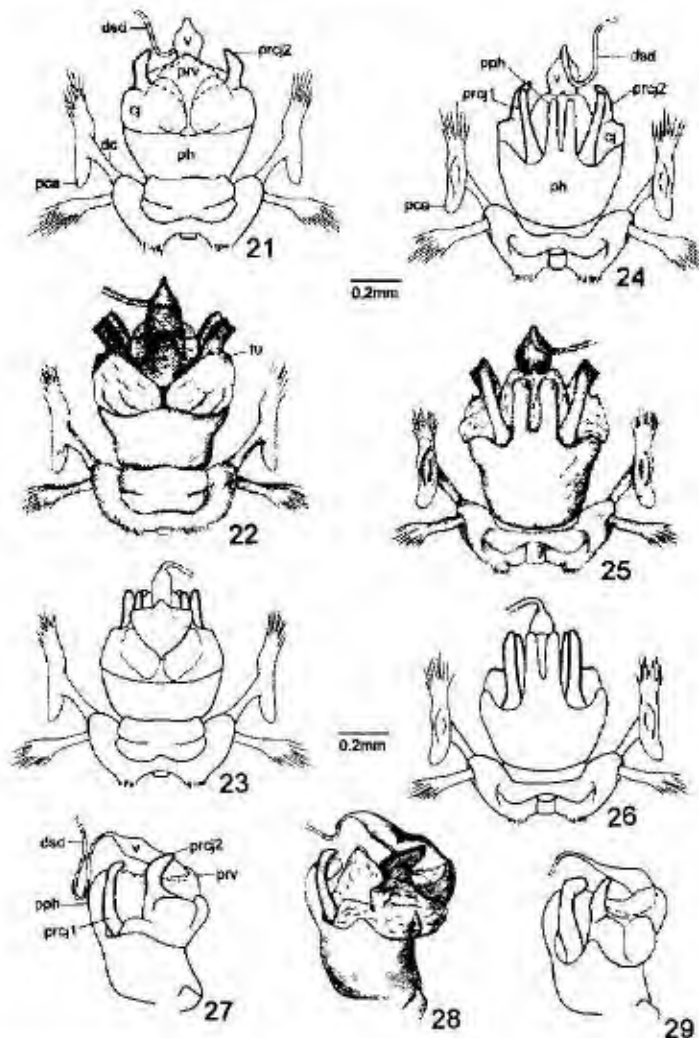
Figs 17-20. Pygophores, lateral view. 17 - *S. acarinalis* sp. n., 18 - *S. meridionalis* sp. n.; 19 - *S. pardidens* sp. n., 20 - *S. tropicalis* sp. n. (sa = superior arms; tp = tooth-like projections of superior layer of ventral rim).

Tumescences of gonocoxites 9 forming a little longer digitiform processes than in *S. acarinatis* sp. n. (Fig. 31). Secondary thickenings of gonapophyses 9 with broad projections. Annular crests convergent. Diameter of ductus receptaculi, just after orificium receptaculi and vesicular area, larger than in the other species. Capsula seminalis globose-ovoid (Fig. 35).

DIFFERENTIAL DIAGNOSIS. For differential diagnosis see key above.

DISTRIBUTION. Argentina (Buenos Aires), Brazil (Santa Catarina).

ETYMOLOGY. Name allusive to geographical distribution.



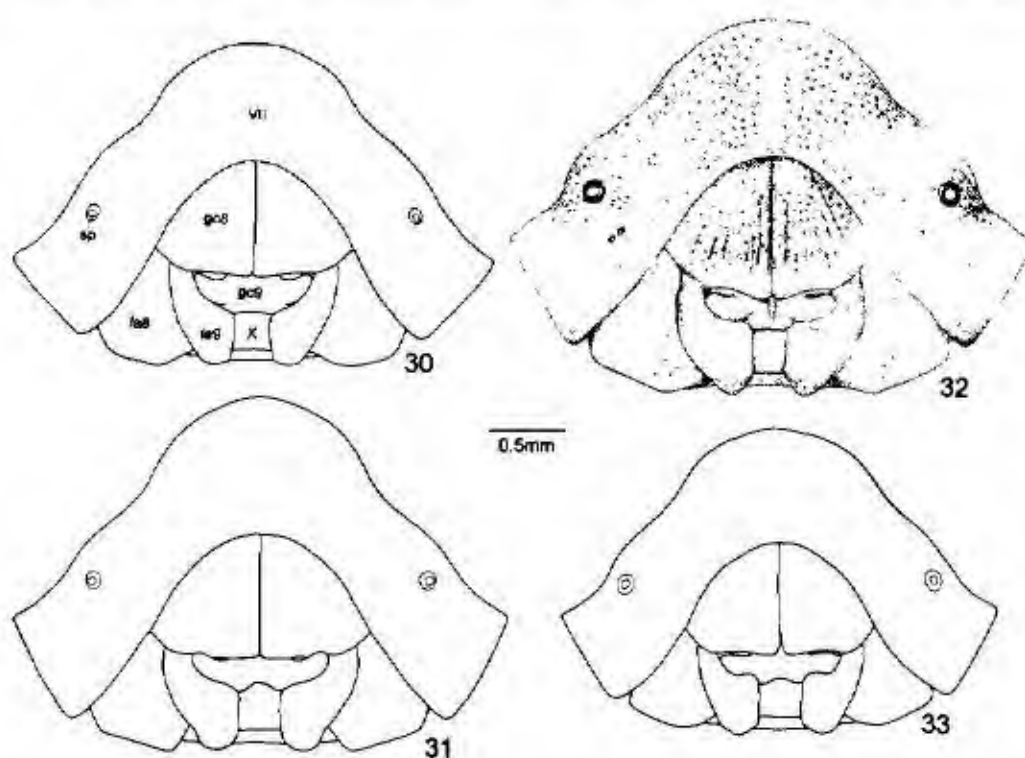
Figs 21-29. Phallus, dorsal, ventral, and lateral view, respectively. 21, 24, 27 - *S. acarinatis* sp. n., 22, 25, 28 - *S. pardidens* sp. n., 23, 26, 29 - *S. tropicalis* sp. n. (cj = conjunctiva; dc = dorsal connectives; dsd = ductus seminis distalis; pca = processus capitati; ph = phallotheca; pph = processus phallothecae; prcj1 = processus conjuntivae 1; prcj2 = processus conjuntivae 2; prv = processus vesicae; tu = tumescence; v = vesica).

***Stysiana pardidens* sp. n.**
(Figs 1, 7, 11, 15, 19, 22, 25, 28, 32, 36)

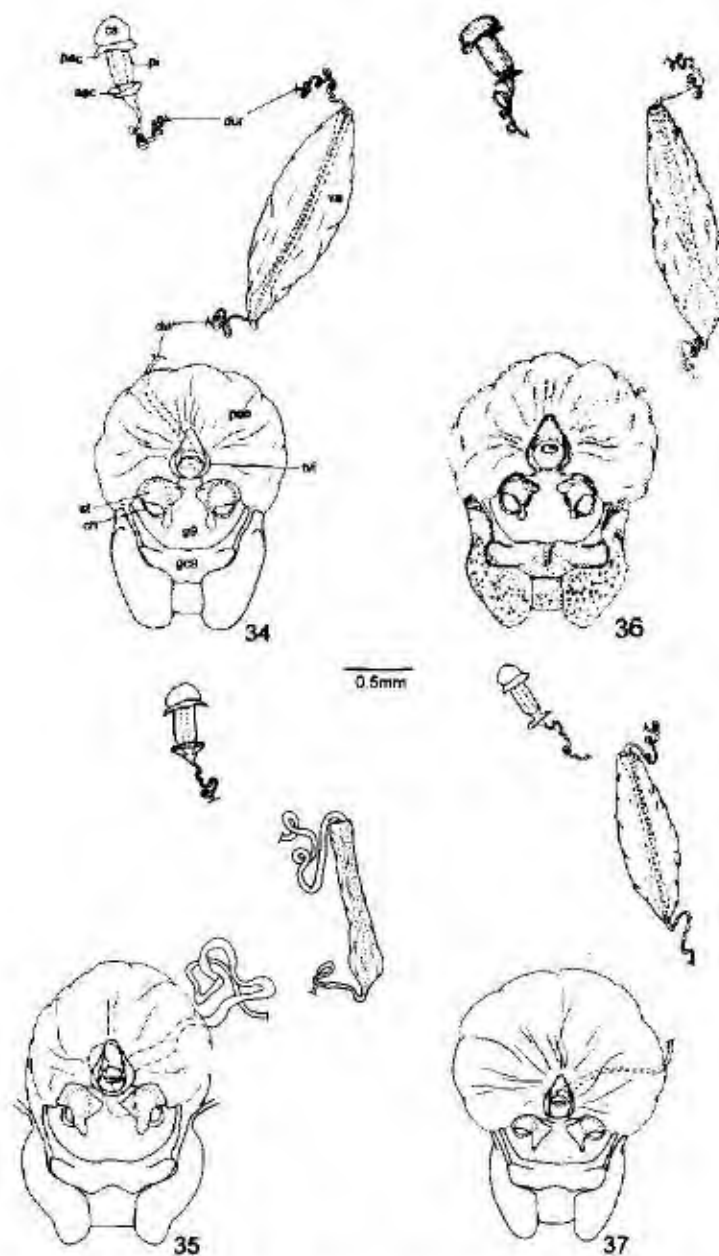
TYPE MATERIAL. Holotype male - PERU San Ramon de Pangoa, 40 km SE Sotipo, 750 m, 24.4.1972, R. T. & J. C. Schuh coll. (AMNH). Paratypes: 1 male and 1 female, same data as holotype (AMNH); 1 female, GUYANA, 3 1909, A. W. Bartlett coll. (BMNH); 3 females, COLOMBIA, Villavicencio, M. L., 19.7.1938, Henry Dybas coll., L. H. Rolston collection (NMNH); 1 female, ibidem, 19.7.1938, T. W. Furry coll., L. H. Rolston collection (NMNH); 1 female, BRAZIL, Rio de Janeiro, Parati, Pedra Branca, 9.12.1941, Berta col. (UFRG); 1 female, Minas Gerais, Viosa (UFRG); 1 male, Santa Catarina, Nova Teutonia, 27° 11'S 52° 23'W, 300-500 m, 1.1976, Fritz Plaumann col. (UFRG); 1 female, ibidem, 10.1975, ibidem.

DESCRIPTION. Jugae contiguous before tylus, divergent at apex; lateral margins clearly toothed just before eyes. Anterolateral angles of pronotum with a long, forwardly directed tooth (Fig. 1). Mesosternum with a well developed keel-like carina, semicircled in outline. Metasternum concave; anterior and posterior margins forming acute angles, anteriorly elevated.

Male. Body length 8.94 (8.61-9.43); abdominal width 4.40 (4.26-4.59); head length 1.91 (1.89-1.97); length before eyes 1.09 (1.07-1.15); width through eyes 2.08 (2.05-2.13); width before eyes 1.26 (1.23-1.31); width between eyes 1.50 (1.39-1.56); distance ocellum-eye 0.36 (0.33-0.41); length



Figs 30-33. Female genital plates. 30 - *S. acarinnatis* sp. n., 31 - *S. meridionalis* sp. n., 32 - *S. pardidens* sp. n., 33 - *S. tropicalis* sp. n. (gc8 = gonocoxites of eighth segment; gc9 = gonocoxites of ninth segment; la8 = laterotergites of eighth segment; la9 = laterotergites of ninth segment; sp = spiracles of seventh segment; VII = seventh segment; X = tenth segment).



Figs 34-37. Gonocoxites, laterotergites and gonapophyses of ninth segment, and ectodermal genital ducts. 34 - *S. acarinatis* sp. n., 35 - *S. meridionalis* sp. n., 36 - *S. pardidens* sp. n., 37 - *S. tropicalis* sp. n. (aac = anterior annular crest; ch = chitinellipson; cs = capsula seminalis; dur = ductus receptaculi; g9 = gonapophyses of ninth segment; gc9 = gonocoxites of ninth segment; pac = posterior annular crest; pco = pars communis; pi = pars intermedialis; st = secondary thickenings of gonapophyses 9; tvi = thickening of vaginal intima; va = vesicular area).

of antennal segments I 0.49; II 0.33; III 1.19 (1.15–1.23); IV 0.94 (0.90–0.98); V 1.19 (1.15–1.23); scutellar length 3.01 (2.95–3.12), scutellar width 2.71 (2.46–2.87); pronotal length 2.02 (1.97–2.13), pronotal width 4.24 (4.10–4.43); corium length 4.15 (4.02–4.43).

Pygophore: postero-lateral angles well developed; dorsal rim not projected. Superior layer of ventral rim of pygophore expanded in rectangular arms. Tooth-like projections of inferior layer of ventral rim far apart from each other (Figs 7, 11, 15, 19). Postero-lateral angles of phallosome developed. Processus phallosomae strongly curved dorsad. Processus conjunctivae 2 broad and flat, in a boot-like structure, in outline (Figs 22, 25, 28).

Female. Body length 9.86 (9.51–10.50); abdominal width 4.66 (4.26–5.00); head length 2.00 (1.89–2.13), length before eyes 1.17 (1.07–1.31); width through eyes 2.15 (2.05–2.30); width before eyes 1.30 (1.23–1.48); width between eyes 1.54 (1.48–1.64); distance ocellum-eye 0.41; length of antennal segments I 0.50 (0.41–0.57); II 0.36 (0.33–0.41); III 1.19 (1.15–1.31); IV 0.87 (0.74–0.90); V 1.13 (1.07–1.23); scutellar length 3.31 (3.12–3.53), scutellar width 2.82 (2.71–2.95); pronotal length 2.14 (1.97–2.30), pronotal width 4.51 (4.35–4.67); corium length 4.39 (4.10–4.76).

Tumescences of gonocoxites 9 forming globose processes, truncate at apex (Fig. 32). Secondary thickenings of gonapophyses 9 with claviform projections. Anterior annular crest turned toward vesicular area of ductus receptaculi. Capsula seminalis in a kidney-like structure (Fig. 36).

DIFFERENTIAL DIAGNOSIS. For differential diagnosis see key above.

DISTRIBUTION. Brazil (Minas Gerais, Rio de Janeiro, Santa Catarina), Colombia, Guyana, Peru.

ETYMOLOGY. Name allusive to the general coloration.

Stysiana tropicalis sp. n.

(Figs 4, 8, 12, 16, 20, 23, 26, 29, 33, 37)

TYPE MATERIAL. Holotype: male – BRAZIL, Maranhão, São Luís, 18.6.1984 (varr 39-39440), A. Brisolia col (MZSP). Paratypes: 1 female, TRINIDAD, 2 mi N Cumata, 14.6.1973, R. Baranowski/ F. O'Rourke/ V. Picchu/ J. Slater colls, donation from J. A. Slater Collection (AMNH); 1 female SURINAM, cultartum, 8.7.1939, Geyskes coll (NMNH); 1 female, Paramaribo, 15.1.1958, P. H. van Doesburg Jr (RMNH); 1 female, BRAZIL, Rondônia, Ouro Preto D'Oeste, 17.1.1985, A. Mendes col (UFRG); 1 female, Maranhão, São Luís, 5.6.1987 (varr 36-3625), A. Brisolia col (UFRG); 1 female, Espírito Santo, Linhares, 9.1971, F. M. Oliveira col (NMNH).

DESCRIPTION. Jugae contiguous before tylus; lateral margins of jugae sinuous. Antero-lateral angles of pronotum with a short, laterally directed tooth (Fig. 4). Anteriorly 2/3 of mesosternum with a moderately elevated carina. Metasternum slightly scavated; anterior and posterior margins forming acute angles, anteriorly elevated.

Male. Body length 7.30 (6.72–7.82); abdominal width 3.90 (3.69–4.10); head length 1.52 (1.48–1.56); length before eyes 0.86 (0.82–0.90); width through eyes 1.68 (1.64–1.72); width before eyes 0.86 (0.82–0.90); width between eyes 1.11 (1.07–1.15); distance ocellum-eye 0.25; length of antennal segments I 0.41; II 0.29 (0.25–0.33); III 0.90; IV 0.49 (0.25–0.74); V 0.94 (0.90–0.98); scutellar length 2.67 (2.46–2.87), scutellar width 2.30 (2.13–2.46); pronotal length 1.72 (1.56–1.89), pronotal width 3.69 (3.44–3.94); corium length 3.53 (3.20–3.85).

Pygophore: postero-lateral angles developed; dorsal rim well projected. Superior layer of ventral rim of pygophore expanded in subtriangular arms. Toothlike projections of inferior layer of ventral rim far apart from each other (Figs 8, 12, 16, 20). Postero-lateral angles of phallosome developed. Processus phallosomae slightly curved dorsad. Processus conjunctivae 2 digitiform, cylindrical (Figs 23, 26, 29).

Female. Body length 7.99 (7.87–8.12); abdominal width 3.87 (3.20–4.10); head length 1.57 (1.48–1.64); length before eyes 0.98 (0.82–1.48); width through eyes 1.75 (1.64–1.80); width before eyes 0.90; width between eyes 1.18 (1.15–1.23); distance ocellum-eye 0.30 (0.25–0.33); length of anten-

nal segments I 0.41; II 0.31 (0.25–0.33); III 0.93 (0.90–0.98); IV 0.72 (0.66–0.74); V 0.90 (0.82–0.98); scutellar length 2.90 (2.79–3.03), scutellar width 2.41 (2.30–2.54); pronotal length 1.75 (1.72–1.80), pronotal width 3.84 (3.69–3.94); corium length 3.69 (3.53–3.94).

Tumescences of gonocoxites 9 moderate, not developed at apex (Fig. 33). Secondary thickenings of gonapophyses 9 with slender projections. Anterior annular crest turned toward vesicular area of ductus receptaculi. Capsula seminalis globose (Fig. 37).

DIFFERENTIAL DIAGNOSIS. For differential diagnosis see key above.

DISTRIBUTION. Brazil (Rondônia, Maranhão, Espírito Santo), Surinam, Trinidad.

ETYMOLOGY. Name allusive to the geographical distribution.

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BOOK REVIEW

CHAIKA S. Yu. *Morfofunktsionalnaya spetsializatsiya nasekomykh-gematofagov [Morpho-functional specialisation of hematophagous insects]* Moscow: KMK Scientific Press, 426 pp, 132 figs, 11 tabs, ISBN 5-87317-043-6

The introductory chapter includes a general consideration on the concept of insect parasitism and characterization of the most important groups of blood-sucking insects – the hematophagous Hemiptera and Diptera, and the Anoplura and Siphonaptera stressing the differences in food uptake and digestion in individual groups.

The main part of the volume is divided into three principal groups of chapters. The first of them, called "The analysis of ultrastructural organization of sensoria systems" (4 chapters) describes the ultrastructural arrangement of visual organs, olfactory organs and contact chemoreceptors. The evolution of these organs is characterized by a significant conservatism in organization of sensory cells. In all the taxa studied, there are only microvillary retinula cells though their variability in both composed and simple eyes is rather higher. Although the set of sensilla types and their numbers are most diverse in free-living bloodsuckers (high in the dipteran hunters for small, dispersed hosts), this conservatism of sensory cells is related to the presence of ciliary structures in their dendrites of sensilla in chemoreceptive, mechanoreceptive hygro- and thermoreceptive organs. The major feature of gustatory sensilla seems to be high sensitivity of sensory cells to adenine nucleotides, mainly to ATP and ADP.

The second part of this book (3 chapters) is devoted to the analysis of ultrastructural and functional features of metabolic systems. Structures of extracellular digestion are shown to vary considerably within different taxa and, in some cases, within individual groups showing different type of parasitism. Significant morphological modifications of digestive system (e.g. the absence of peritrophic membrane, exuberances of midgut cells increasing the contact area of cellular membrane with hydrolysed substances) exist in temporary and permanent ectoparasites (louse-flies, fleas, etc). Some sort of polymorphism of glycocalyx in hematophagous insects is revealed. The set of enzymes of certain subclasses (peptidohydrolases, glycosidases, esterases) depends largely on the phylogenesis of the group. No apparent specialisation in their composition was found except for some esterases. Most hematophagous insects are characterized by a considerable uniformity of Malpighian tubules. However, those of Anoplura and Siphonaptera show some common characters with epithelial cells of Malpighian tubules of arachnids.

The last part of the volume is called "General regularities of morphofunctional specialization of hematophagous insect in connection with the evolution of their trophic patterns and type of parasitism" (4 chapters). It contains a general discussion on plesiomorphic and apomorphic traits of organization, conservatism and specialization, analysis of heterobathism, evolution and type of feeding, and possible origin of insect hematophagy.

The book is concise, technically perfect, with a large number of excellent original electronmicrograms although some graphs would be much improved by a computer processing. The list of more than 750 references seems to be particularly stimulating representing an extensive source of up-to-date knowledge on this topic. I also miss subject and/or scientific names indexes enabling quicker orientation in particular problems. Although having an extensive English summary, the English edition of the volume is urgently needed to disseminate information to a wider range of readers. There is hardly any need to emphasize how useful such a comprehensive treatment is for parasitologists, entomologists and biologists in general.

T. Soldan

**A new genus of apterous Carventinae from Madagascar:
Stysaptera gen. n. with description of two new species
(Heteroptera: Aradidae)***

Ernst HEISS

Research Associate, Tiroler Landesmuseum, 2a Josef-Schraffl-Strasse, A-6020 Innsbruck, Austria

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Abstract. *Stysaptera* gen. n. with the type species *Stysaptera ikalala* sp. n. and a second one *Stysaptera andasibe* sp. n. are described from specimens collected in rainforests at the Island of Nosy Boraha (St. Marie) and Andasibe (Périnet) in East Madagascar. Both species are apterous. A key for the three macropterous and three apterous genera of Carventinae so far known from Madagascar and the Mascarene Islands is given. The new species are figured.

Taxonomy, new genus, new species, Heteroptera, Aradidae, Carventinae, Afrotropic region

INTRODUCTION

The last comprehensive study of the Aradidae of Madagascar and the adjacent Mascarene Islands dates back to Hoberlandt (1957, 1963). Of the subfamily Carventinae he lists 4 genera with 8 species: *Andobocoris* (1), *Bergrothista* (2), *Burgeonia* (4) and *Jarmilaia* (1). In addition only one genus with one species from the Comoro Islands (*Comorocoris testudiformis* Heiss, 1985) and one species from Madagascar (*Burgeonia dilatata* Kormilev, 1974) have been described since (Kormilev & Froeschner 1987).

Among those genera only *Andobocoris* and *Comorocoris* share the condition of complete aptery. Their body structures are highly modified due to the loss of wings and an adaptation to their habitat, the layers of litter and decaying wood on the floor of tropical rainforests.

All apterous Aradidae are particularly endangered by the still wide spread system of shifting cultivation, where successive areas of primary rainforest are burnt and cleared to obtain new land for cultivation. It has been observed on different occasions and localities of North- and East Madagascar, that even those areas where dense secondary forest has grown up, no more apterous Aradidae could be traced when their living habitat has once been destroyed by fire. The small size and the wingless condition limit considerably the range of active distribution which resulted in a very high degree of endemism also in Madagascar.

MATERIALS AND METHODS

The species upon which this study is based have been collected from the underside of logs of leaf bearing trees laying on the floor of rather undisturbed rainforests.

Holotypes are deposited at the Tiroler Landesmuseum Innsbruck (Austria), incorporated as a permanent loan in the authors collection (cEH). Paratypes are also deposited in the collections of Pavel Štys, Charles University,

* Dedicated to my friend Pavel Štys on the occasion of his 65th birthday in recognition of his important contributions to the knowledge of Aradidae.

Key to the genera of Carventinae of Madagascar and the Mascarene Islands

- 1 macropterous 2
- apterous 4
- 2 body surface except membrane with yellow-brownish incrustation concealing the granulate structure beneath, head across eyes (diatone) wider than long. Widely distributed in Africa and Madagascar *Burgeonia* Schouteden, 1919
- body surface without incrustation, head at most as wide as long 3
- 3 larger species, 6.7 mm (male) to 6.8 mm (female), antennae longer about 3.75× as long as the diatone. Endemic to Madagascar *Jarmilata* Hoberlandt, 1957
- smaller species, 4.9mm (male) to 5.9 mm (female), antennae shorter about 3× as long as the diatone. Endemic to Madagascar *Bergrothista* Kirishenko, 1959
- 4 body globular, strongly inflated with testudiform dorsal pattern. Endemic to the Comoro Islands *Comorocoris* Heiss, 1986
- body elongate oval, flat or with moderate median elevation only, surface without such pattern 5
- 5 body flat only slightly elevated along midline, head with rounded postocular portion, anterolateral lobes of pronotum angulate and produced over collar. Endemic to Madagascar *Andobocoris* Hoberlandt, 1963
- body with a distinct increasingly elevated median ridge on fused meso- and metanota + Mtg I+II, sloping posteriorly along tergal disk, head with straight postocular portion, anterolateral lobes of pronotum rounded and shorter than collar. Endemic to Madagascar *Stysaptera* gen. n.

DESCRIPTIONS

Stysaptera gen. n.*

DIAGNOSIS. *Stysaptera* gen. n. is very distinctive among Madagascan apterous Carventinae which can be distinguished from *Comorocoris* and *Andobocoris* by its general habitus and different fusion of thoracic structures and other characters given in the key.

DESCRIPTION. Body form ovate rounded. Surface mat to shiny beneath the whitish incrustation which covers predominantly the furrows and sutures delimiting dorsal and ventral structures.

Head. Of triangular shape, distinctly longer than wide; genae not contiguous anteriorly exceeding apex of clypeus. Antennae slender, more than 2× as long as width of head across eyes (diatone); segment I thickest and longest, II to IV shorter and more slender. Vertex with three longitudinal carinae, postocular portion straightly converging to collar. Eyes lense-shaped, flat. Rostrum shorter than head enclosed in the rostral cavity, rostral atrium closed.

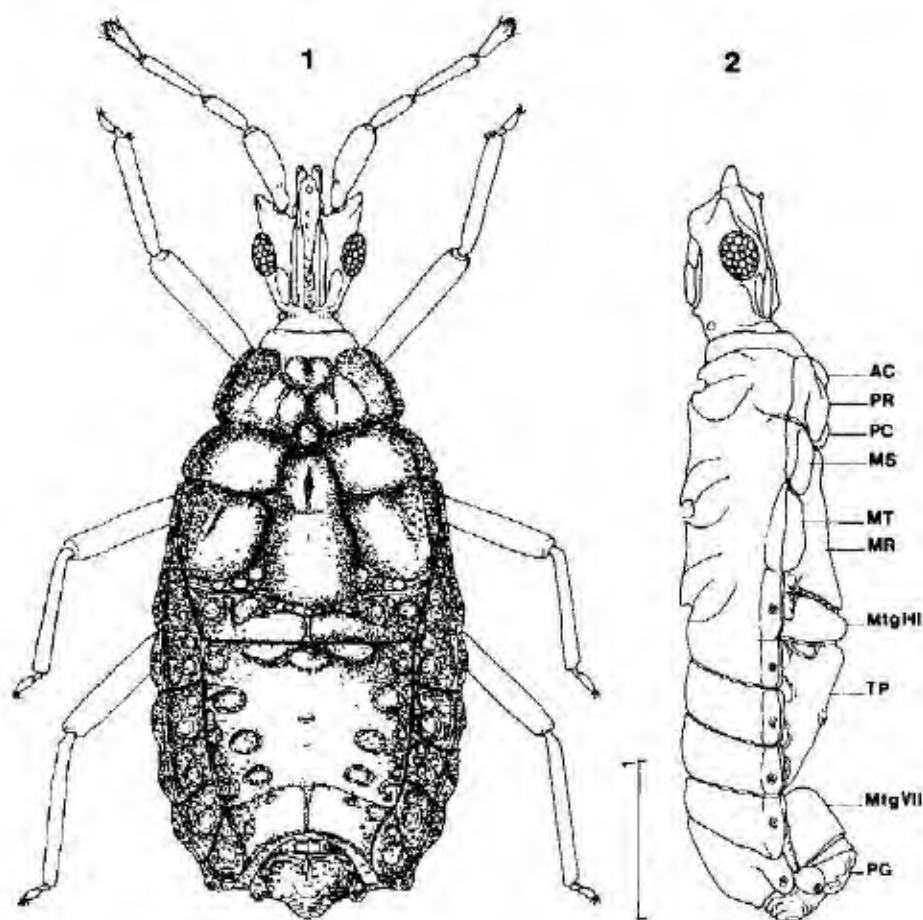
Thorax. Pro- meso- and metanota and first two abdominal tergites fused but marked by deep sutures. Pronotum trapezoidal with rounded anteriorly converging lateral margins, collar distinct. Disk with a deep double y-shaped suture which embraces a larger anterior and a smaller posterior sclerite. Meso- and metanota and first and second abdominal mediotergites (Mtg) completely fused along middle into a subtriangular elevation. Lateral lobes of meso- and metanota subrectangular with longitudinal impressions; lateral margin of mesonotum rounded converging anteriorly, that of metanotum nearly straight. Mtg I+II fused but marked by transverse suture. The triangular connexivum extends forward to posterior margin of mesonotum and is separated by a suture.

Abdomen. Tergal plate consisting of fused Mtg III to VI in continuation of the thoracic ridge triangularly elevated at middle, highest on Mtg III sloping posteriorly. Lateral portions with characteristic pattern of smooth round apodemal impressions. Dorsal scent gland openings marked by

* Since the presentation of this manuscript to the editor, another paper was published with the description of an additional new genus of apterous Carventinae and an updated key, including also *Stysaptera* gen. n. (Heiss 1998).

transverse scars. Dorsoexternal laterotergites (Deltg) III to VI subrectangular slightly raised towards lateral margin, a longitudinal suture separating the visible reflexed ventral laterotergites (Vltg) bearing the spiracles. Deltg II+III fused. Mtg VII strongly raised in male, less in female.

Venter. Pro- meso and metasterna fused but marked by shallow transverse sutures. Prosternum with a median elevation which is widening posteriorly with a single deep puncture at middle. Meso- and metasterna flattened and depressed anteriorly ending in a transverse carina along the segmental border. Their lateral margins with a pair of pointed processes opposing the coxae. Pleural region obliquely rugose. Mediosternites (Mst) I + II + III to VII fused to each other and sternum,



Figs 1-2. *Styroptera ikalalan* gen. n., sp. n. 1 - Holotype of male habitus dorsal view; 2 - ditto lateral view; AC = anterior callus, MR = median dorsal ridge; MS = mesonotum, lateral lobes, MT = metanotum, lateral lobes, Mtg I (II etc.) = mediotergites I (etc.); PC = posterior round callus; PR = pronotum; PG = pygophore; TP = tergal plate. Scale 1 mm

with smooth surface. Mst IV-VI smooth separated by deep transverse grooves. Mst VII in male rugose with an oval smooth longitudinal spot at middle and two (1+1) oblique transverse callosities laterally adjacent to anterior segmental border. Ventral laterotergites rugose. Spiracles II to VIII dorsolateral and visible from above.

Legs. Long, unarmed. Femora not inflated with trochanters fused. Tarsi 2-segmented, claws with curved pseudopulvilli. Preapical comb present on fore tibiae.

Genitalic structures. Male pygophore globose, dorso-caudal portion flattened and rugose. Parameres slender, hook shaped.

TYPE SPECIES. *Stysaptera ikalalao* sp. n.

ETYMOLOGY. Named after the estimated colleague and dear friend Prof. Pavel Štys and referring to the apterous condition; feminine in gender.

DISTRIBUTION. Endemic to Madagascar.

***Stysaptera ikalalao* sp. n.**

(Figs 1-3, 5-10)

MATERIAL EXAMINED. **Holotype:** male, Madagascar, Ile St. Marie (Nosy Boraha), forêt Ikalalao 24-25 X 1995 E. Heiss (cBH); 13 males, 9 females paratypes collected with holotype, cBH, cPS, cLH.

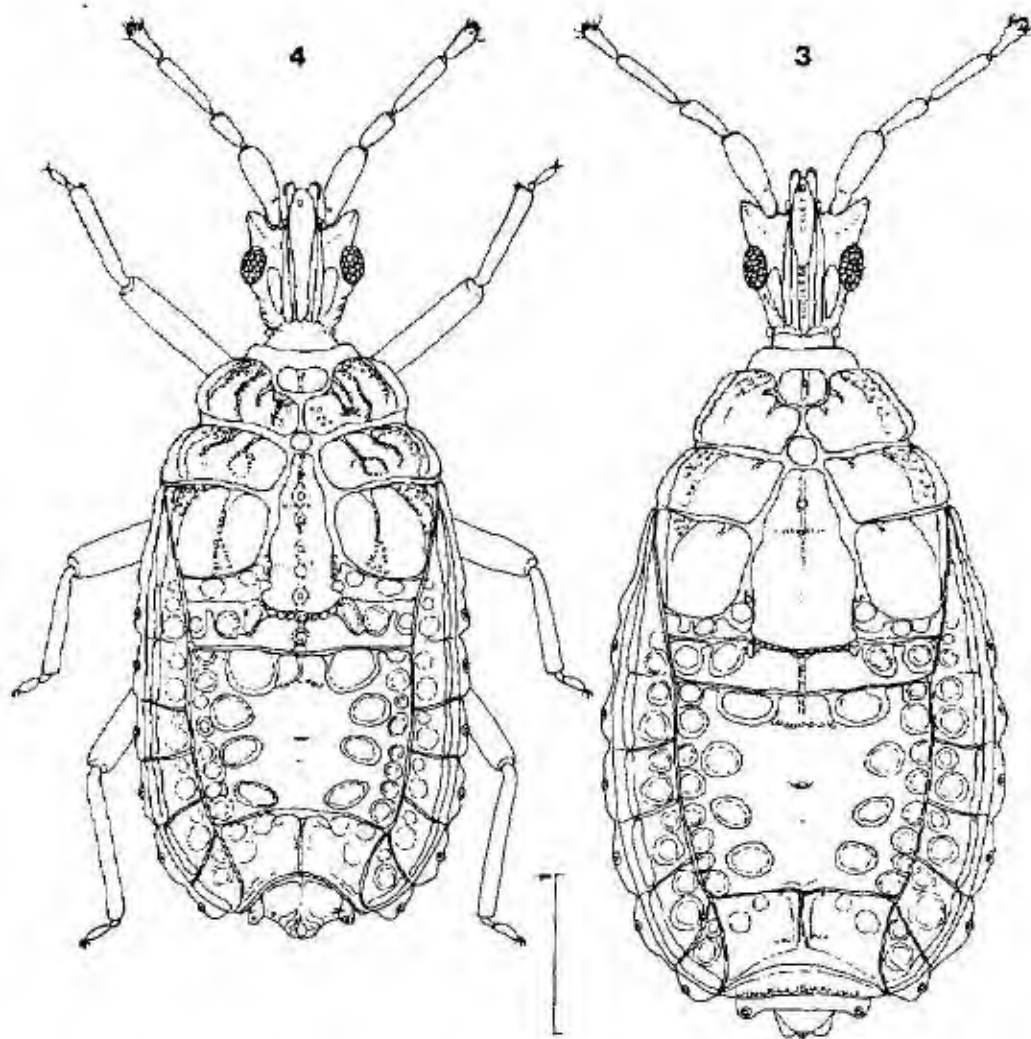
DIAGNOSIS. Distinguished from the second new species of this genus *Stysaptera andasibe* sp. n. by smaller size, the smooth, mat surface of tergal disk, thoracic median ridge and lateral lobes (shiny with deep punctures in *S. andasibe* sp. n.); antennae longer $2.25\times$ as long as width of head ($2.10-2.17\times$ in *S. andasibe* sp. n.) and by subparallel genae (diverging anteriorly in *S. andasibe* sp. n.). **DESCRIPTION.** Male, apterous. Color of body beneath the usual whitish incrustation dark reddish brown, antennae and legs yellowish brown, eyes whitish.

Head. Outline triangular, distinctly longer than wide ($42/30$). Genae subparallel exceeding apex of narrow clypeus which bears dorsally a subapical tubercle, reaching $2/5$ of antennal segment I. Antennae slender, $2.25\times$ as long as width of head ($67.5/30$), segment I club-shaped longest and thickest of all, II short and thinner, slightly widening apically, III longer, cylindrical and thinner as II, IV about as long as II with narrow base and clavate apex which bears long setae. Antennal formula I:II:III:IV = $23:13:18:13.5$. Eyes lense-shaped composed of large ommatidia. Antenniferous lobes triangular, diverging anteriorly, apex blunt. Vertex with a granular median carina in continuation of the clypeus, flanked by 2 (1+1) smooth carinae and smooth oblique callosities laterad; the carinae are limited posteriorly by a curved transverse impression. Postocular region straight, strongly constricted towards collar, 2 (1+1) projecting tubercles are visible laterad of posterior constriction at a lower level. Rostrum shorter than head, rostral groove with carinate borders closed posteriorly, atrium closed slit-like.

Thorax. Pronotum fused to mesonotum but separated by a deep curved suture, $1.72\times$ as wide as long ($50/29$) with a recessed smooth collar anteriorly. Lateral margins rounded and converging towards collar. Disk with an anterior Y-shaped groove which is followed by an inverted Y-shaped one posteriorly, delimiting a larger, longitudinally cleft anterior and a small round posterior sclerite. Lateral lobes with rounded smooth mat surface at middle, longitudinally grooved and punctured laterally.

Mesonotum fused with metanotum and abdominal tergites I-II but marked by deep sutures laterad of a median longitudinal elevated ridge which extends to Mtg II, its surface smooth and mat with 2 deep punctures anteriorly. Lateral lobes of meso- and metanotum subrectangular, with oblique smooth mat elevations on inner side, longitudinally grooved and punctured laterally.

Mtg I+II laterad of median ridge with apodemal impressions flanked by small carinae, lower than lateral lobes of metanotum. Mtg II separated from median thoracic ridge by a transverse suture, its median transversally triangular portion smooth and elevated to level of median ridge, with a longitudinal suture medially. Connexivum triangular projecting forward to posterior margin of mesonotum.



Figs 3-4. 3 - *Stysaptera ikalalao* sp. n., female, dorsal view; 4 - *Stysaptera andasibe* sp. n., holotype X habitus dorsal view. Scale 1 mm.

Abdomen. Tergal plate fused, elevated to level of median ridge anteriorly sloping towards connexivum and posteriorly. Surface smooth mat at middle with deep apodemal impressions laterally. Abdominal scent glands marked by transverse scars. Deitg II+III fused, IV to VI subrectangular, VII triangular, their surface irregularly depressed and rugose. Lateral margin formed by the reflexed narrow portion of the ventral laterotergites bearing dorsolaterally visible spiracles II to VII. Mtg VII strongly raised at middle with a longitudinal suture dorsally. Paratergites VIII small triangular, spiracle VIII dorsolateral and visible from above.

Venter. Structure as in the generic description. Surface of sternite VII in male with smooth mat oval triangular spot at middle and oblique callosities on each side close to anterior segmental border, coarsely granulate elsewhere.

Legs. Shorter than in *Stysaptera ikalalao* sp. n., protibial comb present.

Genitalic structures. Pygophore as figs 5–6; parameres as figs 7–10.

Measurements. Holotype male, length 4.75 mm; width of abdomen across tergite III 2.0 mm; antennae 1.69 mm; diatone 0.75 mm, ratio length of antennae/diatone 2.25.

Female (Fig. 3). Generally as male but larger and abdomen wider. Mtg VII less elevated, tergite VIII wide and transverse with dorsolateral spiracles VIII on laterocaudally rounded lobes. Segment IX narrow, tricuspidate posteriorly.

Measurements. Length 5.50 mm; head l/w 1.15/0.8 mm; pronotum 1.4/0.75 mm; width of abdomen across tergite III 2.6 mm; ratio antennae/diatone 2.25.

ETYMOLOGY. This species is named for the type locality; *ikalalao* is a noun in apposition.

ECOLOGY. *Stysaptera ikalalao* sp. n. was associated with fungi on the humid underside of still bark bearing decaying branches, laying on or in connection with the forest soil, the preferred habitat of most tropical Carventinae.

Stysaptera andasibe sp. n.

(Fig. 4)

MATERIAL EXAMINED. **Holotype:** male, Madagascar, Maromizah S Andasibe (Périnet) 22 X 1995 E.Heiss (cEH); 1 male 1 female paratypes collected with holotype cEH.

DIAGNOSIS. Can be distinguished from *Stysaptera ikalalao* sp. n. by the following characters. Larger, body wider and more stout; rugosities and punctures more extended on thorax; median thoracic ridge with a continuous row of deep punctures along midline; legs shorter.

DESCRIPTION. Slightly larger but very similar to *S. ikalalao* sp. n. so that the description will be concentrated on those characters differing from the latter. Male, apterous. Color of body beneath incrustation more reddish brown, legs and antennae yellowish.

Head. Distinctly longer than wide (42/31.5), genae diverging anteriorly. Antennae shorter, $2.10 \times$ as long as width of head (66/31.5), antennal formula I:II:III:IV = 22:12:19:13. Segment I longest and thickest, II short and thinner, III second longest and thinnest, IV subequal in length to II.

Thorax. Pronotum wider $2.11 \times$ as wide as long at middle (55/26), surface shiny. Median thoracic ridge narrower, extending from anterior margin of mesonotum to posterior margin of Mtg II, surface shiny with 7–8 deep punctures along midline. Meso- and metanota and abdominal tergites I+II fused, with basic structures as in *S. ikalalao* sp. n. but whole not only lateral surface shiny with deep longitudinally arranged punctures. On the median ridge the anterior margin of Mtg II is ill defined by a transverse row of punctures not with a suture as in *S. ikalalao* sp. n.

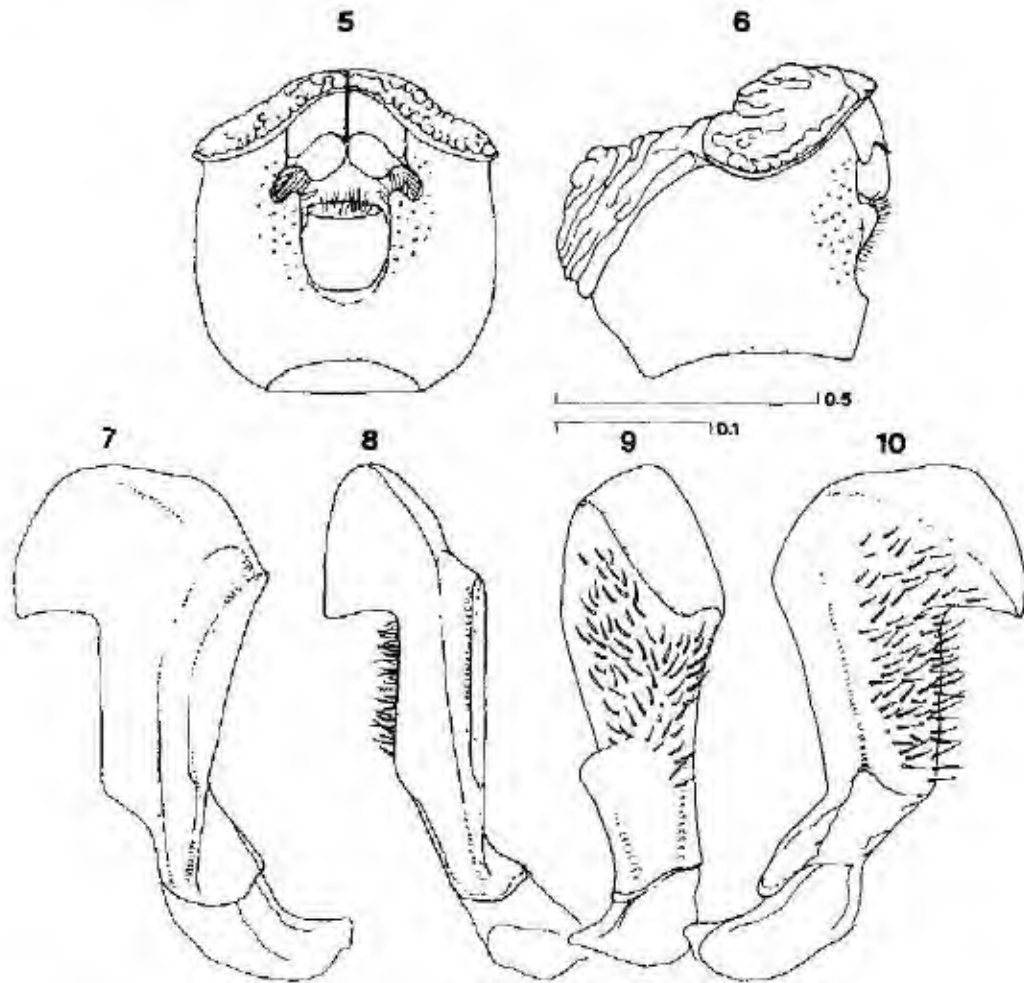
Abdomen. Structure and pattern of apodemal impressions as in the compared species but surface lateral and anterior to a median smooth and shiny oval area on Mtg IV to VI more rugose. Anterior scent gland opening distinct. Spiracles II to VII dorsolateral on reflexed Vltg and visible from above. Paratergites VIII more globular, spiracle VIII dorsolateral and visible from above.

Venter. Structures as described for the genus, sutures of sternal median plate less visible than in *S. ikalalao* sp. n.

Genitalic structures. The single male has not been dissected.

Measurements. Holotype male, length 4.80 mm; width of abdomen across tergite III 2.15 mm; antennae 1.65 mm; diatone 0.79 mm; ratio length of antennae/diatone 2.10

Female. Generally as male except larger and wider body, Mtg VII less elevated, tergite VIII transverse and wide with dorsolateral spiracles VIII on laterocaudal rounded lobes, segment IX narrower tricuspidate posteriorly.



Figs. 5-10 *Stysiptera ikalalao* sp. n. 5 - pygophore dorsal view; 6 - pygophore lateral view; 7 - 10 paramere in different positions. Scale 0.5 mm figs 5,6; 0.1 mm figs 7-10.

MEASUREMENTS. Length 5.75 mm; head w/1 1.17/0.86 mm; pronotum 1.6/0.72 mm; width of abdomen across tergite III 2.6 mm; ratio antennae/diatone 2.17

ETYMOLOGY. Named after Andasibe (formerly Périnet) as a noun in apposition, the type locality of this and several other Madagascan Aradidae described to date.

ECOLOGY. This species was found under similar conditions as *S. ikalalao* sp. n. in the montane rain forest area at about 800 m altitude on the eastern slope of the central N-S mountain range.

DISCUSSION

The present description brings the number of Carventinae from the Madagascan Region to 6 genera and 10 species, the latter are all endemics. This figure seems relatively poor compared with other insect groups associated with forests as Cleridae (467) or Pselaphidae (123), both Coleoptera, or Formicidae (199) which are already relatively old figures after Paulian (1961). In spite of the progressive land use and devastation of originally forested areas it can be expected, that many more new unknown species can still be discovered.

Acknowledgements

I thank Jitka Vilimová (Charles University, Praha) and Miroslav Papáček (University of South Bohemia, České Budějovice) for the invitation to present a paper for this anniversary volume

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The spider-commensal plant bug genus *Ranzovius* (Heteroptera: Miridae: Phyllinae) revisited: Three new species and a revised key, with the description of a new sister genus and phylogenetic analysis

Thomas J. HENRY

Systematic Entomology Laboratory, Plant Sciences Institute, Agricultural Research Service, USDA
c/o National Museum of Natural History, Washington, D. C. 20560-0168, USA

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Abstract. The species *Ranzovius bicolor* sp. n. and *R. brailovskyi* sp. n. from Oaxaca and Morelos, Mexico, and *R. styxi* sp. n. from Paraná, Brazil, are described and associated with spiders of the genus *Anelosimus* Simon, 1891 (Theridiidae). *Ranzovius mexicanus* (Van Duzee, 1923) is synonymized under *R. moerens* (Reuter, 1905), the type of the genus, which is redescribed and associated with *Anelosimus jucundus* (O. P. Cambridge, 1896). The genus *Psallivius* gen. n., considered sister to *Ranzovius* Distant, 1893, is described to accommodate the three conifer-inhabiting phyllines *Psallus flaviclavus* Knight, 1930, *P. piceicola* Knight, 1923, and *P. rubrofemoratus* Knight, 1930. Keys to the species of *Ranzovius* and *Psallivius* gen. n. are given to facilitate recognition, and a phylogenetic analysis is provided to help infer relationships. It is hypothesized that *Psallivius* gen. n. and *Ranzovius* evolved from a Nearctic ancestor, with *Ranzovius* radiating southward into the Neotropics.

Taxonomy, phylogeny, keys, new genus, new species, Heteroptera, Miridae, Phyllinae, *Ranzovius*, *Psallivius*, New World

INTRODUCTION

The discovery of three new species and the holotype of *Ranzovius moerens*, and availability of more specimens of *R. crinitus* from Mexico and *R. fennahi* from Brazil and Panama have prompted me to provide further information on the species of the phylline genus *Ranzovius*, the only mirids known to be obligate spider associates. Prior to this study, seven species were recognized. Henry (1984) revised the genus and summarized the literature, including that having observations on the habits of *R. fennahi* (Carvalho 1954) and *R. californicus* (Davis & Russell 1969). Wheeler & McCaffrey (1984) speculated on the origin of spider commensalism in the genus, provided detailed life-history information, and described the fifth instar of *R. contubernalis*, a species subsequently synonymized with *R. clavicornis* (Henry 1985).

In this paper, I describe *R. bicolor* sp. n. from Oaxaca, Mexico, *R. brailovskyi* sp. n. from Morelos, Mexico, and *R. styxi* sp. n. from Paraná, Brazil; synonymize *R. mexicanus* under *R. moerens*, the type of the genus; and present a revised key to facilitate recognition of species. *R. moerens* is associated with the theridiid spider *Anelosimus jucundus*, *R. styxi* sp. n. with *Anelosimus studiosus*, and *R. crinitus* and *R. bicolor* sp. n. with *Anelosimus* sp. The genus *Psallivius* gen. n., described to accommodate the three North American species *Psallus flaviclavus*, *P. piceicola*, and *P. rubrofemoratus*, is hypothesized as the sister genus of *Ranzovius*.

MATERIALS AND METHODS

All nine species of the genus *Ranzovius* and the three species included in the new genus *Psalleovius* were examined to collect and evaluate character information used in the cladistic analysis. Twelve species-group taxa and 13 characters were used in the analysis. A hypothetical phyline outgroup, based largely on the genus *Platynothus*, was used to help establish character polarity.

The cladistic analysis was performed using Hennig86 (Farris 1988), an IBM PC-based program. The analysis was first calculated using the heuristic mh* algorithm, and then using the mh* and bb* branch-swapping algorithm. This algorithm often finds but does not guarantee the shortest or most parsimonious trees. Three attributes of the cladograms or characters were generated (Tab. 1): consistency index (ci), retention index (ri), and length or number of steps (character-state changes) required to fit the data to the tree.

Characters and measurements were collected using a Wild M5 stereoscopic dissecting microscope with an ocular micrometer. Genitalia were illustrated using a Zeiss compound microscope and drawing tube and micrographs were obtained using an Amray 1810 model scanning electron microscope.

The following abbreviations are used for institutions cited in this paper: AMNH (American Museum of Natural History, New York, R. T. Schuh); CAS (California Academy of Sciences, San Francisco, P. Arnaud); INPA (Inst. Nacional Pesquisas da Amazonia, Manaus, Brazil; V. Py-Daniel); MNR (Museu Nacional, Rio de Janeiro, Brazil), the late J. C. M. Carvalho; TAM (Texas A & M University, College Station, J. C. Schaffner); UFPC (Universidade Federal Paraná, Curitiba, Brazil, A. Sakakibara); UNAM (Instituto de Biología, Universidad Nacional Autónoma de México, México, D. F., H. Brailovsky); USNM (National Museum of Natural History, Smithsonian Institution, Washington, D. C.; R. C. Froeschner and T. J. Henry); ZISP (Zoological Institute, St. Petersburg, I. M. Kozhner); ZMC (Zoologisk Museum Copenhagen; N. M. Andersen).

Ranzovius Distant, 1893

Ranzovius Distant, 1893: 423. Carvalho 1958: 136, Henry 1984: 54, Henry & Wheeler 1988: 495, Schuh 1995: 419. Type species: *Ranzovius crinitus* Distant, 1893. Monotypic.
Nyctella Reuter, 1905: 35. Synonymized by Carvalho 1952: 65. Type species: *Nyctella mourans* Reuter, 1905. Monotypic.

DESCRIPTION. Small, length 1.8 to nearly 2.9 mm, dark colored, clothed with dark simple setae, intermixed on pleural areas of thorax and usually on dorsum with recumbent, silvery, scalelike setae. Head broader than long, in lateral aspect produced anteriorly by a distance subequal to the lateral width of an eye; eyes finely pubescent, nearly touching anterior margin of pronotum. Rostrum extending to metacoxae or beyond. Antenna stout, segment I shortest and thickened, II longest and swollen in both sexes, subequal to or greater than thickness of segment I, length slightly longer than, to shorter than width of head. Pronotum trapeziform, calli weakly defined, scutellum equilateral; hemelytra entire, membrane with two closed cells. Legs typically phyline; tibiae pale with dark spots at bases of spines; claws short, length subequal to diameter of tarsomeres, relatively straight, with hairlike parempodia.

REMARKS. Most species of *Ranzovius* possess sericeous or silky pubescence on the hemelytra. Henry (1984) commented that Carvalho's (1955a) key to genera would not work because sericeous dorsal pubescence was not then a known character for the genus. With the availability of more specimens, I discovered that *Ranzovius fennahi*, the species Carvalho used to construct his key, is, in fact, the only species in the genus that lacks sericeous pubescence on the hemelytra.

All species, including *R. fennahi*, however, possess sericeous pubescence on the pro-, meso-, and metapleura. This character will allow recognition of all species belonging to *Ranzovius* and supports the monophyly of the genus in the tribe Phylini when taken in combination with the short, thickened 2nd antennal segment that is at least as thick as antennal segment I and has the length less than or only slightly greater than the width of the head across the eyes, the small fuscous to black body (length always less than 3.00 mm, except for *R. crinitus*), the short, slender claws, the unique, twisted, sigmoid vesica, and the spider web-inhabiting behavior.

Also, it now appears that the claws of *Ranzovius* are shorter and straighter than those of other phylines examined. Previously, Henry (1984) had investigated the claws and determined that in comparison to members of the nabid genus *Arachnocoris* Scott, 1881, *Ranzovius* claws did not appear modified. While not modified to the extent of some other symbionts, such as Plokiophilidae (Eberhard et al. 1993) or species of *Arachnocoris* (Henry 1984), they may still reflect a mechanical adaptation for walking on nonsticky areas of spider webs.

The position of *Ranzovius* within the tribe Phylini has never been investigated. Superficially, species of the genus resemble members of the genus *Psallus* Fieber, 1858, based on the overall dark coloration of many species, silvery, sericeous setae, and spots at the bases of the tibial spines. The genitalia found in members of *Ranzovius*, however, differ considerably from those of *Cimex haematodes* (Gmelin, 1790), the type species of *Psallus*, as well as from the genitalia of many other Nearctic species now included in *Psallus* (Henry & Wheeler 1988).

Three North American conifer-inhabiting species currently placed in *Psallus* possess male genitalia and other characteristics that indicate a sister-group relationship with species of *Ranzovius*. *Psallus flaviclavus*, *P. piceicola*, and *P. rubrofemoratus* share with species of *Ranzovius* a similar male vesica, pale areas at the base of the cuneus, and sericeous setae on the hemelytra and pleural areas of the thorax.

These species differ from those in *Ranzovius* in having a plesiomorphic slender 2nd antennal segment, a shorter frontal and ventral extension of the head, and much longer, more curved claws (lengths much greater than diameters of the respective tarsomeres). Clearly derived is the secondary gonopore possessing numerous tiny spicules, supporting recognition of a separate monophyletic group. In addition, they are not obligate spider-web inhabitants as are all species of *Ranzovius*, an adaptation unique in the family Miridae (and found elsewhere in the Heteroptera only in the genus nabid *Arachnocoris* and the family Plokiophilidae). While members of the *Psallus piceicola* group are associated strictly with their coniferous hosts, species of *Ranzovius* are restricted only to their spider host's webs that may be found on a broad array of plants.

Revised key to the species of *Ranzovius*

- 1 Antennal segment I pale yellowish brown 2
 - Antennal segment I always fuscous or black 3
- 2 Second antennal segment pale yellowish brown, base of corium and usually base of clavus pale, scutellum uniformly fuscous or black, Mexico (Oaxaca) 4
 - Second antennal segment fuscous or black, hemelytra corium and clavus uniformly fuscous or black, apical 1/3 of scutellum pale, Mexico (Morelos) 5
R. bicolor sp. n.
R. brailowskyi sp. n.
- 3 Length of antennal segment II equal to or greater than width of head across eyes 4
 - Length of antennal segment II shorter than width of head, not greater than width of vertex and a single eye combined 5
- 4 Antennal segment II strongly swollen, greatest diameter 1/2 or more width of vertex, vesica with 2 sclerotized spiculi, western United States (California) 6
R. californicus (Van Duzee)
 - Antennal segment II more slender, greatest diameter about 1/3 width of vertex, vesica without any apparent apical spiculi, eastern United States (Tennessee) 7
R. agelenopsis Henry
- 5 Hemelytra with only simple sericeous setae, lacking silvery sericeous pubescence, base and apex of cuneus fuscous or black, at most with a trace of pale at the apex of embolium, Brazil (Amazonas, Para), Panama, Suriname, Trinidad 6
R. jennah Carvalho
 - Hemelytra bearing simple and silvery sericeous pubescence, apex of cuneus and embolium and, often, base of cuneus pale or white 7
- 6 Base of cuneus with a wide, pale or white mark, extending from outer margin across cuneal fracture to membrane 7
 - Base of cuneus fuscous or black, at most with a narrow pale or white mark at apex of embolium not extending from outer margin across cuneal fracture to membrane 8

- 7 Larger species, length 2.28–2.32 mm in males, 2.60–2.68 mm in females; length of antennal segment III greater than width of vertex; Mexico (Mexico, DF, Michoacan, Oaxaca, Puebla, Veracruz). *R. erinitus* Distant
- Smaller species, length 1.86–2.10 mm in males, 2.08–2.28 mm in females; length of antennal segment III equal to or less than width of vertex; widespread in eastern United States. *R. clavicornis* (Knight)
- 8 Length of antennal segment II greater than length of head; length of segment III greater than width of vertex; Panama, Venezuela *R. moerens* (Reuter)
- Length of antennal segment II less than length of head; length of segment III less than width of vertex; southern Brazil (Paraná) *R. stylus* sp. n.

***Ranzovius agelenopsis* Henry, 1984**

Ranzovius agelenopsis Henry, 1984: 58, Wheeler & McCaffrey 1984: 76, Henry & Wheeler 1988: 495, Schuh 1995: 419

DIAGNOSIS. This species appears to be sister to the western *R. californicus* in having an agelenid host and strongly thickened 2nd antennal segment. It is separated from that species in lacking spiculi on the vesica and by the more slender 2nd antennal segment that is subequal to about 1/3 the diameter of the vertex. *R. agelenopsis* appears to be the only species in the genus that lacks spiculi on the vesica.

DISTRIBUTION. Known only from Tennessee where it was taken in the webs of *Agelenopsis pennsylvanicus* (C. L. Koch, 1843) (Agelenidae).

***Ranzovius bicolor* sp. n.** (Figs 1–10)

DIAGNOSIS. This species (Fig. 1) can be distinguished from all other members of the genus by the pale first and second antennal segments and the pale areas at the bases of the clavus and corium. **DESCRIPTION.** Males (n=5): Length 2.00–2.24 mm, width 0.92–1.00 mm. Head: Length 0.42–0.44 mm, width 0.50–0.52 mm, vertex 0.30–0.32 mm. Rostrum: Length 1.02–1.08 mm, extending beyond metacoxae, nearly to base of genital capsule. Antenna: Segment I, length 0.18–0.20 mm; II, 0.36–0.38 mm, thickness at middle 0.06 mm; III, 0.26–0.32 mm; IV, 0.22–0.24 mm. Pronotum: Length 0.36–0.38 mm, basal width 0.74–0.80 mm.

Females (n=5): Length 2.24–2.56 mm, width 0.96–1.06 mm. Head: Length 0.46–0.48 mm, width 0.50–0.52 mm, vertex 0.32–0.34 mm. Rostrum: Length 1.06–1.12 mm, extending beyond metacoxae to 6th abdominal segment. Antenna: Segment I, length 0.20–0.22 mm; II, 0.36–0.40 mm, thickness at middle 0.06 mm; III, 0.26–0.34 mm; IV, 0.20–0.24 mm. Pronotum: Length 0.36–0.40 mm, basal width 0.78–0.84 mm.

General coloration dark brown or fuscous, with extensive pale areas at the base of the hemelytra, thickly clothed with recumbent golden-brown setae, intermixed on hemelytra and scutellum with thickened, silvery, sericeous setae (Fig. 5). Head (Fig. 2) dark brown with recumbent golden-brown setae, intermixed with shorter more silvery pubescence, especially along inner margins of eyes and vertex; eyes reddish brown, with numerous short, erect setae. Antennal segment I and II uniformly pale testaceous or yellowish brown, except for narrow dark base of segment I; segments III and IV more dusky or brownish. Pronotum (Fig. 2) uniformly dark brown, thickly set with rather long, recumbent golden-brown setae. Scutellum uniformly fuscous. Hemelytra dark brown to fuscous, with the base of the corium, apical margin of the embolium, and extreme apex and basal 1/2 or less of clavus pale (pale area extending to about apex of scutellum), some specimens with pale areas at bases of clavus and corium slightly less extensive; cuneus fuscous with the apex pale and sometimes with a narrow translucent, but not whitish, area at base; membrane smoky brown to fuscous, veins

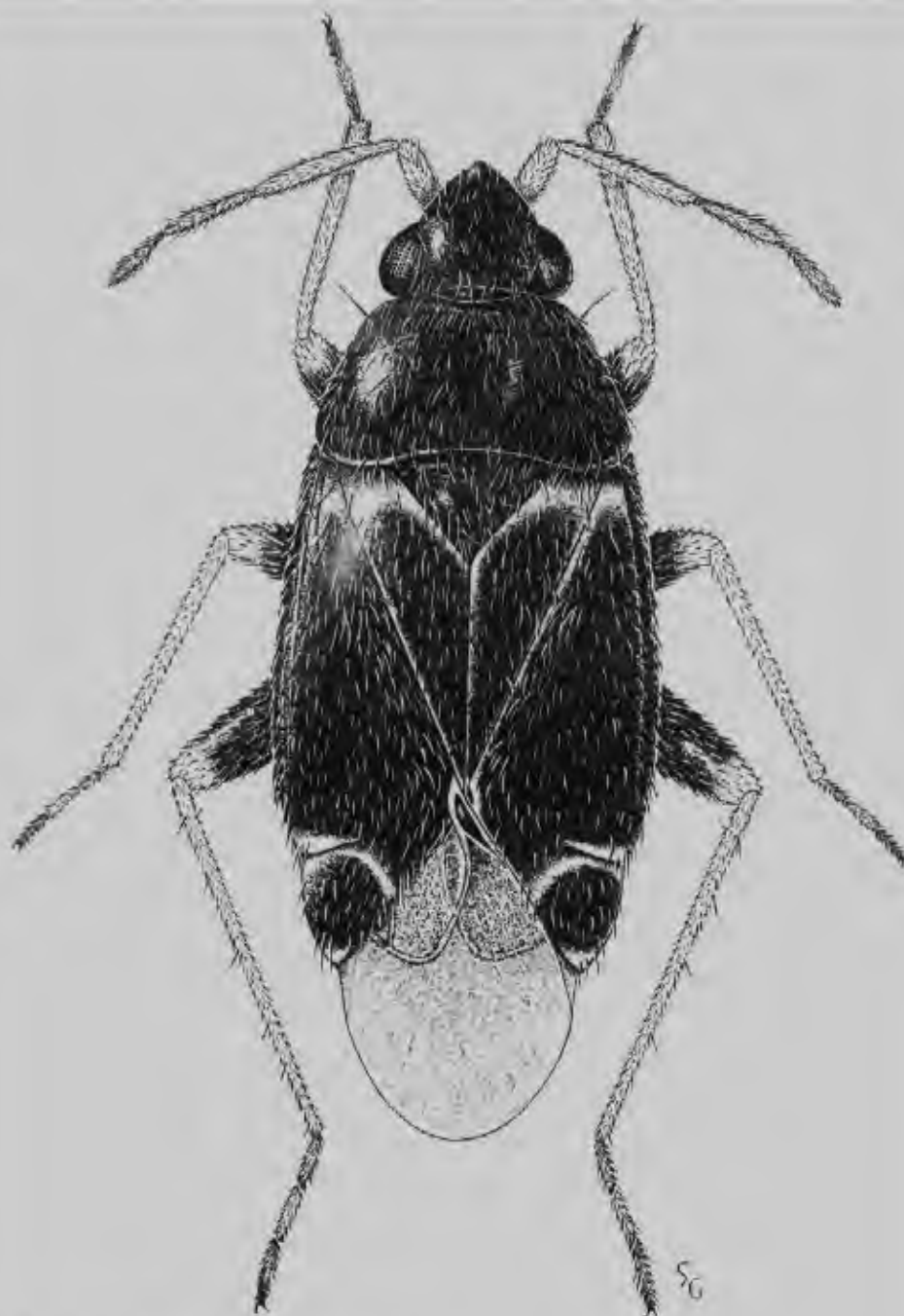
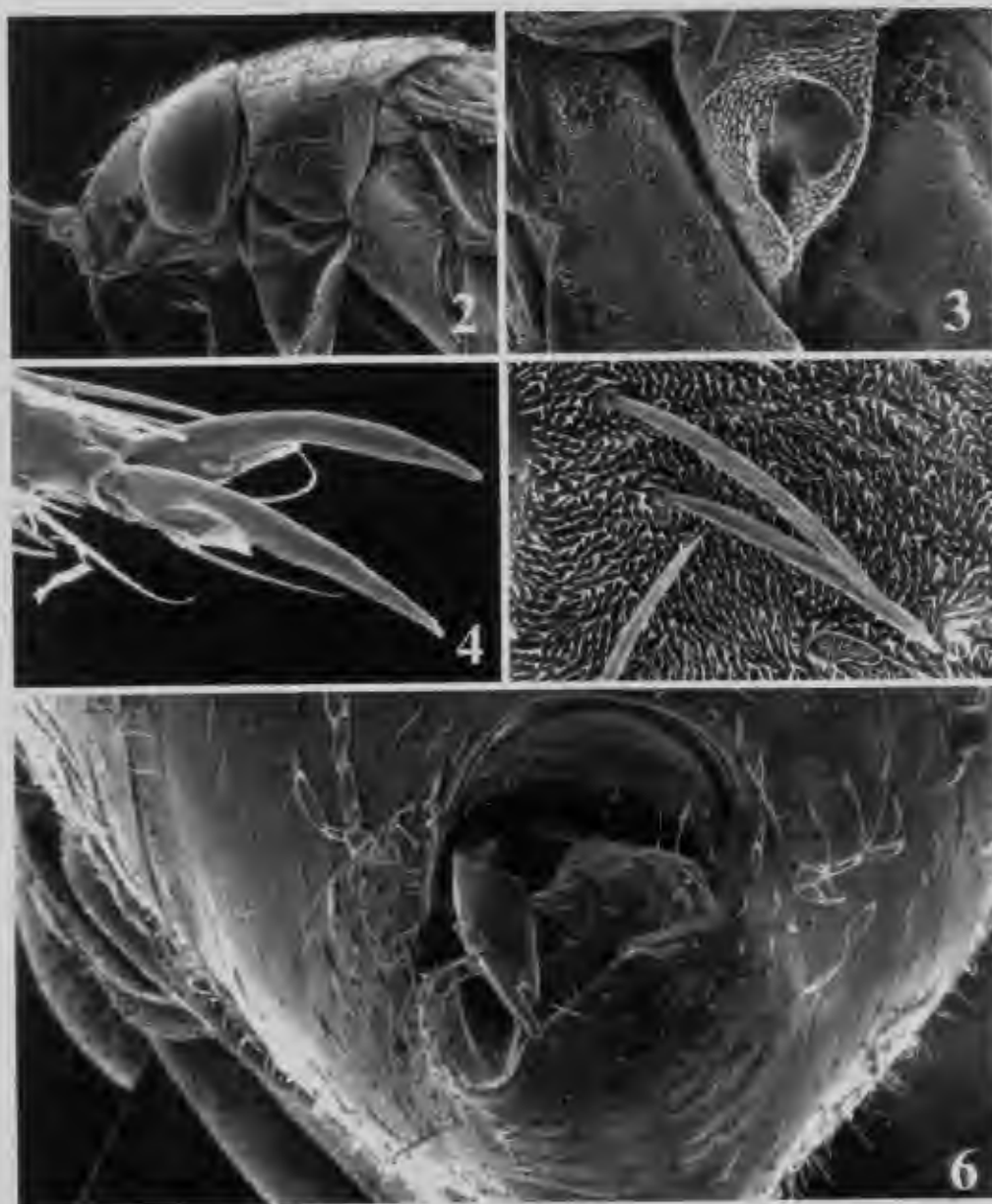


Fig. 1. Dorsal adult habitus of *Ranisoxenus bicolor* sp. n.



Figs 2-6. Scanning electron micrographs of *Ranziulus bicolor* sp. n. 2 - head and pronotum, lateral aspect (145 \times); 3 - ostiolar area (408 \times); 4 - claw (1500 \times); 5 - scalelike setae on pleura (1350 \times); 6 - male genital capsule, caudal aspect (208 \times).

pale. Ventral surface dark brown, fuscous, or nearly black, more shiny than dorsum; propleura narrowly pale along ventral edge, pleural areas of thorax thickly set with patches of silvery, sericeous setae, abdomen with recumbent golden setae. Ostiolar area (Fig. 3) mostly fuscous, becoming more pale on anterior lobe of auricle. Coxae fuscous; femora fuscous with apices pale; tibiae pale testaceous, spines fuscous, with diffuse dark spots at bases of metatibiae; tarsi pale testaceous or yellowish brown; claws (Fig. 4) brown.

Male genitalia: Genital capsule (Fig. 6); left paramere (Fig. 7); right paramere (Fig. 8); vesica (Fig. 9); phallosome (Fig. 10).

TYPE SPECIMENS. **Holotype**, male, Mexico, Oaxaca, Monte Alban, 22 Sept. 1989, taken in webs of *Anelosimus* sp. on *Ficus* sp., E. Barrera, T. J. Henry, and I. M. Kerzhner (USNM). **Paratypes**: 15 males, 13 females, same data as for holotype (UNAM, USNM, ZISP).

ETYMOLOGY. This species is named *bicolor* for the unusual bicolored hemelytra having the base of the clavus and corium pale, contrasting with the remaining dark areas.

REMARKS. This species was found together with *R. crinitus* in webs of *Anelosimus* sp., on a large, open-growing *Ficus* sp., heavily infested with Cuban laurel thrips, *Gynaikothrips ficorum* (Marchal, 1908). In the field, *R. bicolor* sp. n. was mistaken as teneral adults of *R. crinitus*, rather than a different species, because of the paler, bicolored hemelytral pattern.

Ranzovius brailovskyi sp. n.

(Figs 11–14)

DIAGNOSIS. This species is distinguished from other species of the genus in having the apical 1/3 of the scutellum pale. It is most similar to *R. bicolor* sp. n. in having the first antennal segment pale, but can be separated by the dark 2nd antennal segment and apically pale scutellum.

DESCRIPTION. Male ($n=5$): Length 2.40–2.88 mm, width 1.04–1.08 mm. Head: Length 0.46–0.52 mm, width 0.54–0.56 mm, vertex 0.28–0.30 mm. Rostrum: Length 1.04–1.06 mm, extending to bases of metacoxae. Antenna: Segment I, length 0.20–0.24 mm; II, 0.50–0.52 mm, thickness at middle 0.08 mm; III, 0.34–0.36 mm; IV, 0.24–0.26 mm. Pronotum: Length 0.44–0.48 mm, basal width 0.92–0.96 mm.

Female ($n=5$): Length 2.40–2.96 mm, width 1.04–1.12 mm. Head: Length 0.50–0.52 mm, width 0.54–0.56 mm, vertex 0.30–0.32 mm. Rostrum: Length 0.96–1.10 mm, extending to bases of metacoxae. Antenna: Segment I, length 0.22–0.24 mm; II, 0.42–0.46 mm, thickness at middle 0.06 mm; III, 0.30–0.34 mm; IV, 0.18–0.20 mm. Pronotum: Length 0.42–0.44 mm, basal width 0.88–0.96 mm.

General coloration dark brown or fuscous, thickly clothed with relatively long, recumbent, golden-brown setae, intermixed with patches of silvery sericeous setae on cuneus, clavus, and corium. Head dark brown, somewhat shiny, with some brown setae, intermixed with short, silvery pubescence on frons and tylus; eyes reddish, with scattered, short, erect setae. Antennal segment I pale, sometimes tinged with reddish; segment II fuscous to black; segments III pale to dusky, and IV fuscous to black. Pronotum dark brown, somewhat shiny, with relatively long, recumbent golden-brown setae; each anterior angle with a long, dark, bristlelike seta. Scutellum dark brown to fuscous, with apical 1/3 pale. Hemelytra fuscous, slightly paler at apex of clavus and narrowly pale at apex of embolium; cuneus fuscous, pale at apex and with a trace of pale along cuneal fracture; membrane uniformly dark or fuscous, veins paler. Ventral surface fuscous to black, somewhat shiny, pleural areas of thorax with numerous linear patches of silvery sericeous pubescence; abdomen sparsely set with short recumbent brown setae. Coxae fuscous; femora fuscous with apices pale; tibiae and spines pale or yellowish brown, some basal spines with diffuse dark spots at bases; tarsi yellowish brown, apex of last tarsomere and claws brown.

Male genitalia: Left paramere (Fig. 11); right paramere (Fig. 12); vesica (Fig. 13); phallosome (Fig. 14).

TYPE SPECIMENS. **Holotype**, male, Mexico, Morelos, Cuautla, 20 Dec. 1989, H. Brailovsky, taken in webs of unknown spider (UNAM). **Paratypes**: 7 males, 6 females, same data as for holotype (UNAM, USNM).

ETYMOLOGY. This species is named in honor of my good friend and collector of this species, Dr Harry Brailovsky, who also provided me with much support during a trip (September 1989) to Mexico where *R. bicolor* sp. n. was discovered.

Ranzovius californicus (Van Duzee, 1917)

Excentricus californicus Van Duzee, 1917: 284

Ranzovius californicus Carvalho 1955a: 224 (as synonym of *R. moerens*), Carvalho 1958: 136 (as synonym of *R. moerens*), Henry 1984: 60, Henry & Wheeler 1988: 496, Schuh 1995: 419.

Ranzovius moerens: Knight 1958: 35 (in part), Davis & Russell 1969: 262.

DIAGNOSIS. This species shares with *R. agelenopsis* the long, thickened 2nd antennal segment that is subequal to the width of the head across the eyes and an agelenid spider association. *Ranzovius californicus* is distinguished from *R. agelenopsis* by the thicker 2nd antennal segment that is about 1/2 the diameter of the vertex.

DISTRIBUTION. *Ranzovius californicus* is known only from California where it is found in webs of *Hololena curta* (McCook, 1894) [Agelenidae].

Ranzovius clavicornis (Knight, 1927)

Psallus clavicornis Knight, 1927; Carvalho 1958: 118

Excentricus mexicanus Blatchley 1926: 962 (in part).

Ranzovius (= *Excentricus* [sic]) *clavicornis*: Mead 1984: 2.

Ranzovius contubernalis Henry 1984: 61, Wheeler & McCaffrey 1984: 68. Synonymized by Henry 1985: 1130.

Ranzovius clavicornis Henry 1985: 1130, Henry & Wheeler 1988: 496, Schuh 1995: 419.

DIAGNOSIS. This species is similar to *R. crinitus* but can be distinguished by its smaller size (1.86–2.10 mm in males; 2.08–2.28 mm in females), proportionately short 3rd antennal segment, and more slender spiculi on the vesica, as noted by Henry (1984).

DISTRIBUTION. *Ranzovius clavicornis* has been reported over a broad area of the United States, including Arizona, Connecticut, District of Columbia (Washington, DC), Florida, Louisiana, Maryland, North Carolina, Tennessee, Texas, and Virginia (Henry & Wheeler 1988). Kansas and South Carolina are new U.S. state records.

ADDITIONAL SPECIMENS EXAMINED. **United States: Kansas**: 2 males, 1 female, Montgomery Co., Elk City Lake, 6 October 1994, H. Guarisco coll., taken in *Anelosimus studiosus* (Hentz 1850) [Theridiidae] webs (USNM), 4 males, 1 female, Kansas, Labette Co., Big Hill Lake, 22 Sept. 1996, M. Guarisco coll., taken in *Anelosimus studiosus* webs (USNM). **South Carolina**: 3 males, Lancaster Co., Lancaster, 15 May 1988, A. G. Wheeler, Jr., on crape myrtle (USNM).

Ranzovius crinitus Distant, 1893

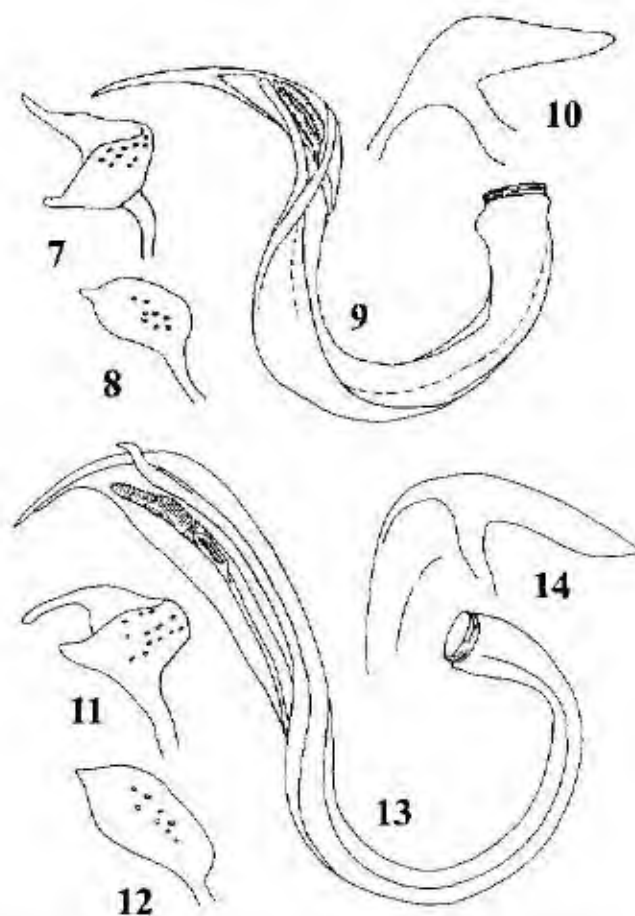
Ranzovius crinitus Distant, 1893: 423, Carvalho 1954: 96, Henry 1984: 63, Henry & Wheeler 1988: 495, Eborhard et al. 1993: 12, Schuh 1995: 420.

Nyctella lunifera Reuter, 1908: 175. Synonymized by Carvalho 1954: 96.

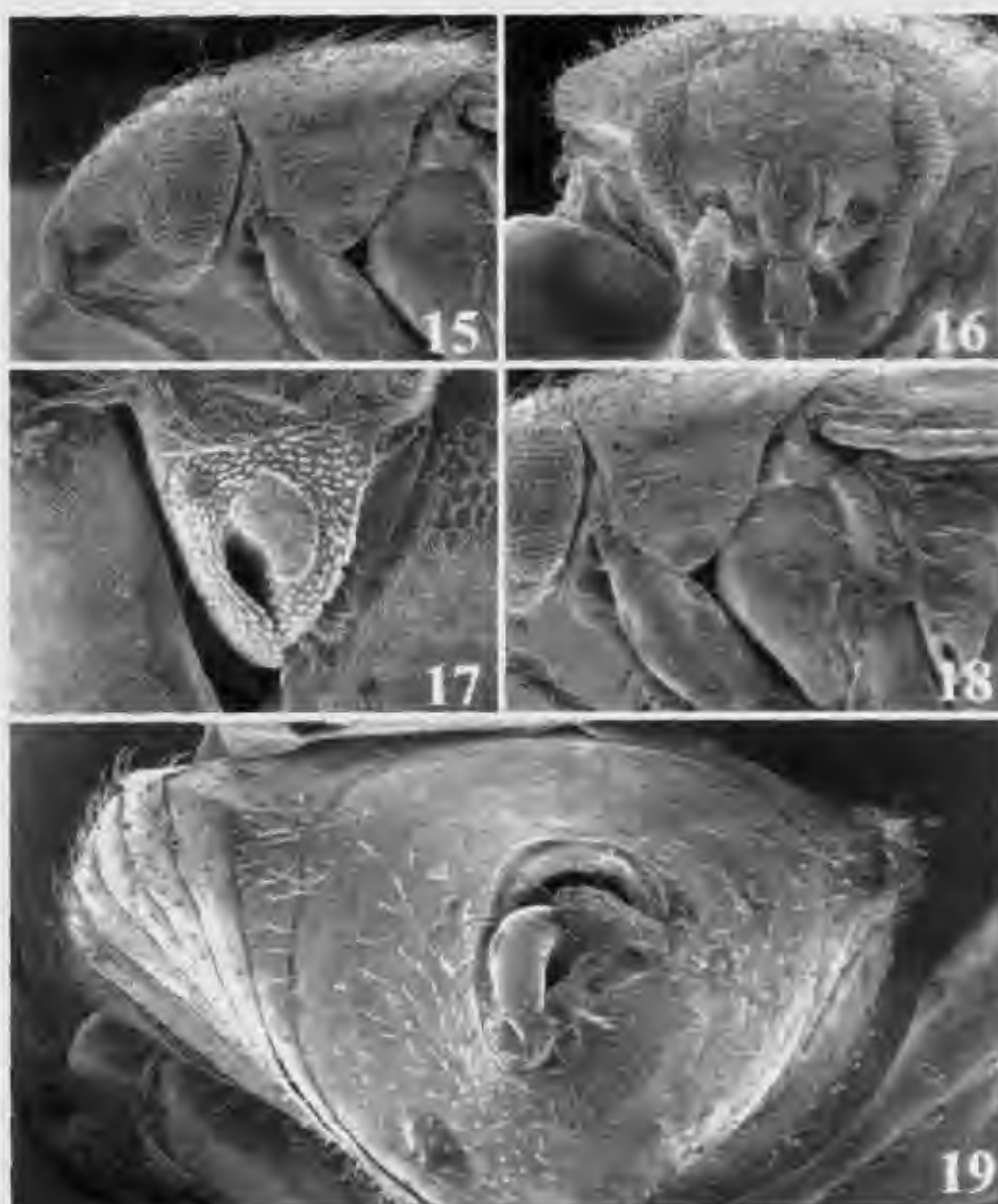
DIAGNOSIS. This species is most similar to *R. clavicornis* in having pale markings at the apex of the corium and base of the cuneus, but *R. crinitus* differs in its overall larger size (2.3–2.7 mm vs. 1.8–2.3 mm), the proportionately longer antennal segment III, and the structure of the male vesica.

DISTRIBUTION. Reported from Costa Rica (Eberhard et al. 1993) and the Mexican states of Guerrero, Puebla, and Veracruz (Henry 1984, Schuh 1995). New state records for Mexico are Mexico D. F., Michoacan, and Oaxaca.

ADDITIONAL SPECIMENS EXAMINED. **Mexico:** Mexico D. F.: 2 males, 6 females, Col-del Valle, 10 Feb. 1990, H. Brailovsky (UNAM, USNM). **Michoacan:** 1 female, 6 mi. n. Chieran, July 7-8, 1985, Jones & Schaffner (TAM). **Oaxaca:** 28 males, 20 females, Monte Alban, 22 Sept. 1989, E. Barrera, T. J. Henry, and I. M. Kerzhner, taken in webs of *Aneides* sp. (Theridiidae) on *Ficus* sp. infested with *Gynaikothrips ficorum* (UNAM, USNM, ZIL). **Puebla:** 1 female, Apuleo (north of Zacapoaxtla) at light, July 22, 1987, Kovarik & Schaffner (TAM). **Veracruz:** 1 male, 3 mi. ne. Huatusco, July 22, 1985, Jones & Schaffner (TAM).



Figs 7-14. Male genitalia of *Ranzovius* spp. *R. bicolor* sp. n., 7-9. 7 - left paramere, 8 - right paramere, 9 - vesica, 10 - phallotheca. *R. brailovskyi* sp. n., 11-14. 11 - left paramere, 12 - right paramere, 13 - vesica, 14 - phallotheca.



Figs 15–19. Scanning electron micrographs of *Rangovius vysi* sp. n. 15 – Head and pronotum, lateral aspect (157 \times). 16 – Head, anterior aspect (158 \times). 17 – Ostiolar area (515 \times). 18 – Pleural area of thorax showing scalelike setae (163 \times). 19 – Male genital capsule, caudal aspect (108 \times).

***Ranzovius fennahi* Carvalho, 1954**

Ranzovius fennahi Carvalho, 1954: 93, Carvalho 1958: 136, Henry 1984: 64, Schuh 1995: 420

DIAGNOSIS. This species is readily separated from all other species of *Ranzovius* by the uniformly dark cuneus lacking a pale mark at the base and by the absence of sericeous setae on the hemelytra.

DISTRIBUTION. This species has been reported from Brazil, French Guiana, Panama, Suriname, and Trinidad (Henry 1984). Ecuador is a new country record. In 1985, I took this species in great abundance in the large webs of *Anelosimus eximius* (Keyserling, 1884) [Theridiidae] on the INPA campus in Manaus, and in 1996, Dawn Southard found *R. fennahi* in *A. eximius* webs in Ecuador.

ADDITIONAL SPECIMENS EXAMINED. **Brazil:** 35 males, 22 females, Amazonas, Manaus, 27 Nov.–8 Dec. 1985, T. J. Henry coll., taken in webs of *Anelosimus eximius* (INPA, MNR, USNM); 15 males, 10 females, Pará, Carajás, Jan. 1986, J. C. M. Carvalho coll. (MNR, USNM). **Ecuador:** Napo Prov., Sierrazul, 2200 m, SW of Baeza, 0°40'S 77°55'W, 17 June 1996, D. Southard, in webs of *Anelosimus eximius* (USNM) [specimens examined but subsequently misplaced, numbers therefore not recorded]

REMARKS. Henry (1984) erred in the last paragraph (p. 64) by stating that *R. fennahi* could be recognized "... by the long 2nd antennal segment that is subequal to or longer than the width of the head." This sentence should have read "by the short 2nd antennal segment that is shorter than the width of the head," as is stated in the identification key.

***Ranzovius moerens* (Reuter, 1905)**

(Figs 20–23)

Nyctella moerens Reuter, 1905: 26, Henry & Wheeler 1988: 495.

Ranzovius moerens: Carvalho 1954: 95 (in part), Carvalho 1955b (in part), Carvalho 1958: 136 (in part), Knight 1968: 35 (in part), Henry 1984: 65, Schuh 1995: 420.

Excentricus mexicanus Van Duzee, 1923: 163, Blatchley 1926: 962 (in part) Synonymized by Carvalho 1955b: 224, resurrected by Henry 1984: 65. **REVISED SYNONYMY**

Ranzovius mexicanus: Henry 1984: 65

DIAGNOSIS. *Ranzovius moerens* is most similar to *R. styxi* sp. n., but can be distinguished by the long 2nd antennal segment that is longer than the length of the head, the long 3rd antennal segment that is longer than the width of the vertex, the slender spiculi of the vesica, the distribution (Central and northern South America), and the association with *Anelosimus jucundus* (O. P. Cambridge, 1896) [Theridiidae].

DESCRIPTION. Males (n=3): Length 2.44–2.68 mm, width 1.00–1.04 mm. Head: Length 0.42–0.44 mm; width 0.50–0.52 mm; vertex 0.30–0.32 mm. Rostrum: Length 1.14–1.16 mm, extending to apex of metacoxa. Antenna: Segment I, length 0.22–0.24 mm; II, 0.42–0.44 mm, thickness at middle 0.06 mm; III, 0.36–0.40 mm; IV, 0.28–0.30 mm. Pronotum: Length 0.40–0.44 mm; width at base 0.76–0.82 mm.

Females (n=5): Length 2.48–2.84 mm, width 1.06–1.12 mm. Head: Length 0.42–0.46 mm, width 0.50–0.52 mm, vertex 0.30–0.32 mm. Rostrum: Length 1.14–1.18 mm, extending just beyond metacoxa to base of 4th abdominal segment. Antenna: Segment I, length 0.22–0.24 mm; II, 0.42–0.44 mm, thickness at middle 0.08 mm; III, 0.38 mm for all; IV, 0.26–0.28 mm. Pronotum: Length 0.42–0.44 mm, basal width 0.80–0.86 mm.

General coloration uniformly, somewhat shiny, fuscous to black, except for narrow, transverse, pale apex of embolium (but not base of cuneus) and apex of cuneus. Membrane fumate, except for a small transparent area adjacent to apex of cuneus. Dorsum thickly clothed with recumbent brown setae, intermixed with silvery sericeous setae on head, pronotum, scutellum, and hemelytra; sericeous

setae on head, pronotum, and scutellum shorter and finer; lateral margins of pronotum, base of head, and antennal segment I with long, black, bristlelike setae. Eyes reddish and distinctly pubescent. Antenna fuscous to black; segment III and IV pale brown, but more whitish at bases and apices; setae recumbent, intermixed with longer, more erect, setae equal to or longer than diameter of segments. Undersurface fuscous or black; abdominal segments with a transverse row of setae along each posterior margin, genital capsule more uniformly pubescent; pro-, meso-, and metapleura with silvery sericeous setae. Ostiolar auricle infuscated with anterior lobe whitish. Coxae and femora fuscous; tibiae and apices of femora pale yellowish brown; tibial spines black, spines on meso- and metatibiae with diffuse fuscous spots at bases; tarsi and claws pale yellowish brown.

Male genitalia: Left paramere (Fig. 20); right paramere (Fig. 21); vesica (Fig. 22) with two slender spiculi, one apical and one subapical and directed upward; phallosome (Fig. 23).

DISTRIBUTION. Mexico and Venezuela (Henry 1984). New country records are Dominican Republic, Ecuador, and Panama. Schuh's (1995) listing of this species from Arizona and California was clarified by Henry (1984, 1985) as misidentifications of *R. clavicornis* and *R. californicus*, respectively.

TYPE SPECIMEN. Study of the unique female holotype from Caracas, Venezuela (ZMC) [label data: 1, "188"; 2, "22/9/11, Caracas"; 3 (red label), "Type"; 4, "Nytella n. gen. moerens n. sp. O. M. Reuter det."; 5 (red label, here added), "Holotype female Nyctella moerens Reuter."] clearly indicates that *R. mexicanus* Distant [holotype, CAS] (Henry 1984) is a junior synonym of *R. moerens*.

OTHER SPECIMENS EXAMINED. **Dominican Republic:** 1 female, intercepted at J. F. Kennedy International Airport, New York, from Dominican Republic, 23 Oct 1981, on citrus (USNM). **Ecuador:** Napo Prov., Sierrazul, 2200 m, SW of Baeza, 0°40'S 77°55'W, 17 June 1996, D. Southard, in webs of *Anelosimus jucundus* (USNM) [specimens examined but subsequently misplaced; numbers therefore not recorded]. **Panama:** 4 males, 11 females, Panama Prov., 23 Aug., 27 Aug., 6 Oct., 29 Oct., and 26 Nov. 1983, W. Nentwig coll., taken in webs of *Anelosimus jucundus* (MNR, USNM).

DISCUSSION. Henry (1984) commented that based on the original description of *R. moerens* he could not separate *R. fennahi* from *R. moerens*, and suggested that they might prove to be synonyms. Now, with the study of the holotype of *R. moerens*, the accumulation of a long series of *R. fennahi* from Manaus, Brazil, and a collection of both from Panama, I am able to distinguish these quite different species. *Ranzovius fennahi* lacks pale marks on the cuneus and sericeous setae on the hemelytra, and has the primary spiculum hooked apically, whereas in *R. moerens* the apex of the cuneus is pale, the hemelytra possess sericeous setae, and the primary spiculum of the vesica is straight.

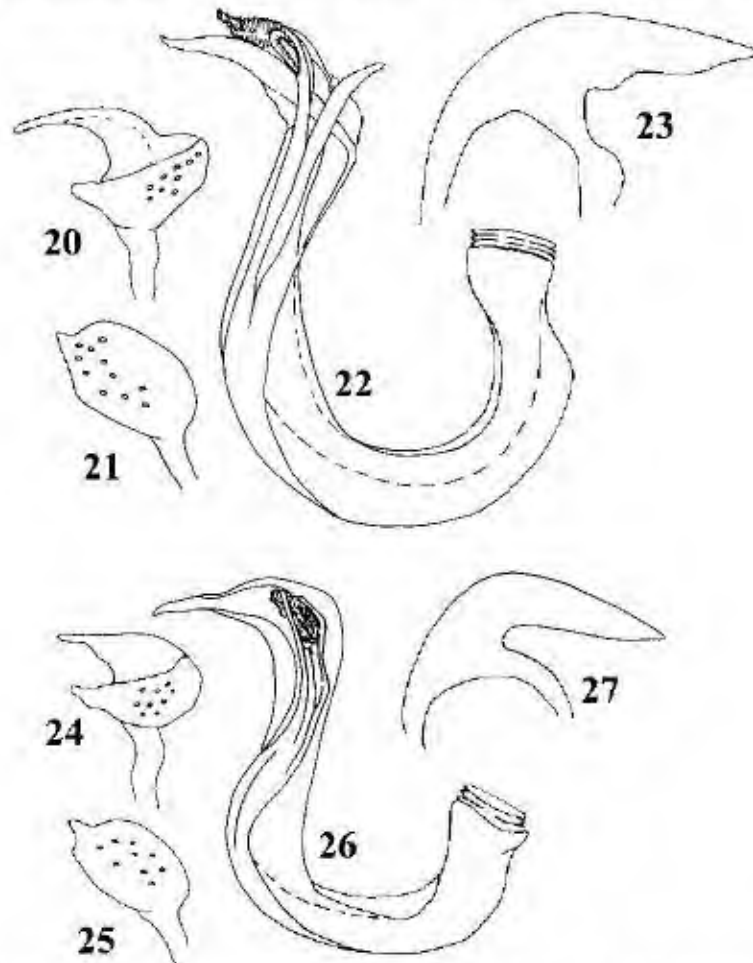
Nearly all of the specimens of *R. moerens* at hand were collected in the webs of *Anelosimus jucundus*. This spider, reported to occur from northern Mexico to Argentina (Levi 1963), is the fifth arachnid associated with the genus *Ranzovius*.

Recent collections of *R. fennahi* and *R. moerens* by Dawn Southard (Department of Entomology, University of Maryland, College Park) in Ecuador provide good additional evidence that these bugs are quite specific in their spider associations. All of her collections of *R. fennahi* were in *A. studiosus* webs and all collections of *R. moerens* were from *Anelosimus jucundus* webs. Collections from Panama, however, showed some mixing of species. Several specimens of *R. fennahi* were found with *R. moerens* in *Anelosimus jucundus* webs. It is not known if both species of *Ranzovius* actually were in *Anelosimus jucundus* webs, or if the specimens were inadvertently mixed in the field after being collected with different spiders. Close proximity of the spider hosts could also explain this mixing. Wheeler & McCaffrey (1984) found both *R. clavicornis* (Knight) and *R. agelenopsis* Henry in webs of *Agelenopsis pennsylvanicus* in Tennessee, but in this case, both spiders were present in the same shrubbery, suggesting accidental wandering by the mirids. All other known collections of *R. clavicornis* are from *Anelosimus studiosus* webs.

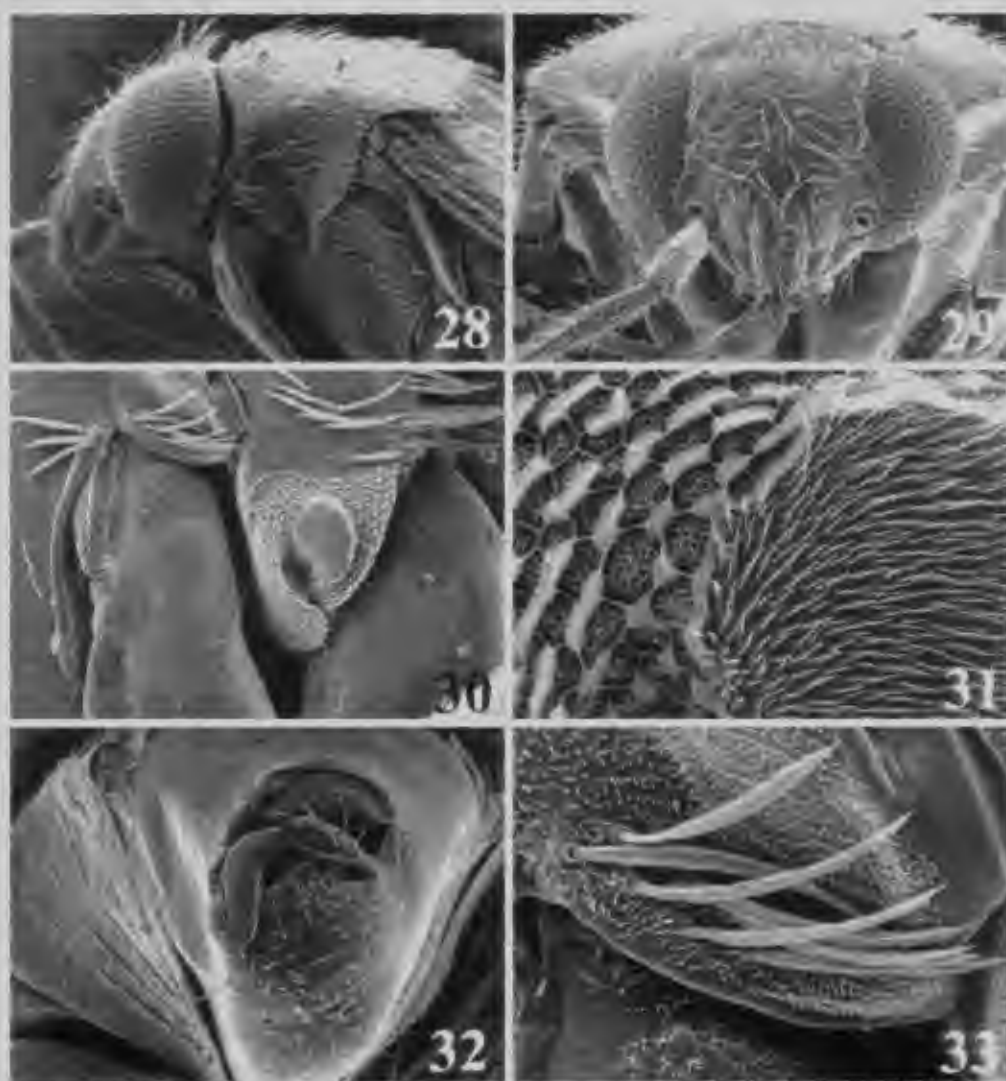
***Ranzovius stysi* sp. n.**
(Figs 15–19, 24–27)

DIAGNOSIS *Ranzovius stysi* sp. n. is most similar to *R. moerens*, but can be distinguished by the shorter 2nd antennal segment that is shorter than the length of the head, the shorter 3rd antennal segment that is shorter than the width of the vertex, the more slender spiculi of the vesica, its distribution (southern Brazil), and association with *Anelosimus studiosus*.

DESCRIPTION. Males ($n=5$): Length 1.88–2.28 mm; width 0.90–0.92 mm. Head: Length 0.38–0.40 mm; width 0.48–0.50 mm; vertex 0.30 mm for all. Rostrum: Length 0.94–0.98 mm, extending to apex of metacoxa. Antenna: Segment I, length 0.18–0.20 mm; II, 0.32–0.36 mm, thickness at middle 0.06 mm; III, 0.24–0.26 mm; IV, 0.18–0.20 mm. Pronotum: Length 0.34–0.36 mm; basal width 0.72–0.74 mm.



Figs. 20–27 Male genitalia of *Ranzovius* spp. *R. moerens* (Reuter), 20–23: 20 – left paramere, 21 – right paramere, 22 – vesica, 23 – phallosome. *R. stysi* sp. n., 24–27: 24 – left paramere, 25 – right paramere, 26 – vesica, 27 – phallosome.



Figs 28-33. Scanning electron micrographs of *Psallonyx piceicola* (Knight). 28 - head and pronotum, lateral aspect (136 \times). 29 - head, anterior aspect (142 \times). 30 - ostiolar area (306 \times). 31 - higher magnification of ostiolar mycoid structures and auricle (magnification not recorded). 32 - male genital capsule, caudal aspect (193 \times). 33 - scutellike setae on pleuron (1160 \times).

Females (n=5): Length 2.12–2.48 mm, width 1.14–1.24 mm. Head: Length 0.40–0.46 mm, width 0.52–0.56 mm, vertex 0.32–0.34 mm. Rostrum: Length 0.98–1.04 mm, extending to apex of metacoxa. Antenna: Segment I, length 0.20–0.22 mm; II, 0.38–0.40 mm; III, 0.26–0.28 mm; IV, 0.20–0.22 mm. Pronotum: Length 0.40–0.46 mm, basal width 0.82–0.92 mm.

General coloration uniformly, somewhat shiny, fuscous to black, except for a narrow pale to whitish mark across apex of embolium (but not at base of cuneus) and at the apex of the cuneus. Membrane fumate. Head dark brown (Figs 15, 16). Dorsum clothed with recumbent yellowish-brown setae; hemelytra intermixed with silvery sericeous setae. Antenna black; segment III pale at base, becoming darker apically, segment IV dark brown, more infuscated than III; clothed with short recumbent brownish setae, intermixed with longer, more semierect setae, some equal to or longer than diameter of segment. Ostiolar area (Fig. 17). Undersurface fuscous to black; abdomen clothed with recumbent yellowish-brown setae; pro-, meso-, and metapleura thickly set with silvery sericeous setae (Fig. 18). Legs: Coxae and femora black, tibiae and apices of femora pale yellowish or yellow brown, tibial spines black, bases of metatibial spines with diffuse black spots. Tarsi mostly yellowish, with apical half of tarsomere III and claws dark brown or fuscous.

Male genitalia: Genital capsule (Fig. 19); left paramere (Fig. 24); right paramere (Fig. 25); vesica (Fig. 26); phallosome (Fig. 27).

TYPE SPECIMENS. Holotype: male, Brazil, Paraná, Curitiba, Universidade Federal do Paraná campus, 19–26 Oct. 1985, T. J. Henry coll., taken in the webs of *Anelosimus studiosus* (UFPC). Paratypes: 26 males, 30 females, same data as for holotype (MNR, UFPC, USNM).

ETYMOLOGY. This species is named after my good friend and colleague, Prof. Pavel Štys, on the occasion of his 65th birthday and in honor of his productive career in heteropterology, which has included a new species of Plokiophilidae, another spider-web inhabiting taxon.

DISCUSSION. This species was taken in the webs of *Anelosimus studiosus* that were abundant on several dozen ornamental trees bordering a parking lot on the Federal University campus at Curitiba. Most trees had 2–4 webs up to a foot (30.48 cm) in diameter that were built around foliage and small branches and contained much debris, most of which was dead leaves. *Ranzovius stysi* sp. n. adults and the red nymphs (instars I–V) were numerous in all webs observed.

This species represents a distribution nearly 1,500 miles farther south than any previously known species, suggesting that additional records and/or species are likely to be discovered in the geographically diverse regions of central South America between Paraná, Brazil, in the south and Ecuador and Amazonas, Brazil, in the north.

Psallivius gen. n.

Type species: *Psallus piceicola* Knight, 1923.

DIAGNOSIS. As noted in the discussion under *Ranzovius*, this new genus is recognized by the overall dark color, pale border around the base of the cuneus, the slender pale antennae, and by the numerous spicules on the secondary gonopore of the vesica. Two of the three members of this genus are known to inhabit conifers in North America.

DESCRIPTION. Brown to fuscous, clothed with dark simple setae, thickly intermixed on dorsum and pleural areas of thorax with recumbent, silvery, scalelike setae. Head broader than long; in lateral aspect, lateral width of eye greater than lateral distance frons extends anteriorly in front of eye; eyes finely pubescent, nearly touching anterior margin of pronotum. Rostrum extending to metacoxae or beyond. Antennae slender, segment I shortest, segment II longest, slightly shorter, to distinctly longer than width of head, diameter subequal to that of segment I, III and IV most slender, III

distinctly longer than IV. Pronotum trapeziform, shiny, impunctate, calli weakly developed, scutellum equilateral. Hemelytra entire, membrane with two closed cells (arcoles). Legs typically phylline, tibiae pale with dark spots at bases of spines, claws longer than diameter of respective tarsomeres, weakly curved, with hairlike parempodia.

ETYMOLOGY. This new genus is formed from the prefix "Psall," taken from the generic name *Psallus* to reflect the historical, but not phylogenetic, association of the included species and from the suffix "ovius", taken from *Ranzovius*, to which this genus is closely related. The gender is masculine.

Key to species of *Psallovius* gen. n.

- 1 Length of antennal segment II less than width of head across eyes *P. flaviclavus* (Knight)
- Length of antennal segment II greater than width of head across eyes 2
- 2 Rostrum extending to bases of metacoxae, femora, except for pale apices, bright red *P. rubrofemoratus* (Knight)
- Rostrum extending beyond metacoxae to at least the 3rd abdominal segment, all femora, except for pale apices, dark brown to fuscous *P. piceicola* (Knight)

Psallovius flaviclavus (Knight, 1930) comb. n.

(Figs 34–37)

Psallus flaviclavus Knight, 1930: 130; Henry & Wheeler 1988: 493; Polhemus 1994: 133; Schuh 1995: 405.

DIAGNOSIS. This species is very similar to *P. piceicola* in overall coloration, but can be distinguished by the short 2nd antennal segment that is shorter than the width of head across the eyes.

DESCRIPTION. Males (n=4). Length 2.72–2.84 mm. Head Width 0.64–0.66 mm, vertex 0.32 mm. Rostrum Length 1.28–1.32 mm, extending onto abdomen beyond 3rd or 4th segments. Antenna Segment I, length 0.20–0.24 mm, II, 0.56–0.60 mm, III, 0.44–0.46 mm, IV, 0.28–0.36 mm. Pronotum Length 0.44–0.46 mm, basal width 0.94–1.00 mm.

Female (n=1). Length 2.88 mm, width 1.32 mm. Head Width 0.68 mm, vertex 0.34 mm. Rostrum Length 1.30 mm. Antenna Segment I, 0.24 mm, II, 0.56 mm, III, 0.44 mm, IV, 0.34 mm. Pronotum Length 0.46 mm, basal width 0.94 mm.

Overall coloration brown to dark brown. Head dark shiny brown. Pronotum, mesoscutum, and scutellum dark shiny brown. Antenna uniformly pale yellow, segment II tinged with red on some specimens, segments III and IV sometimes becoming infuscated. Hemelytra uniformly brown, somewhat red tinged on some specimens, clavus slightly paler, apex of embolium and apex and base of cuneus pale yellow, membrane translucent brown, veins pale. Ventral surface dark brown to fuscous, ostiolar area brown, sometimes red tinged. Coxae dark brown, femora dark brown with pale apices, tibiae and claws yellowish brown.

Male genitalia: left paramere (Fig. 34), right paramere (Fig. 35), vesica (Fig. 36), phallosome (Fig. 37).

HOST. Rocky mountain yellow pine, *Pinus ponderosa* Douglas ex Lawson et C. Lawson var. *scopulorum* Engelm. (Knight 1930).

DISTRIBUTION. Known only from Colorado.

SPECIMENS EXAMINED. United States: Colorado. Holotype male, allotype female, 4 paratype males, Estes Park, Aug. 24, 1925, H. H. Knight, on *Pinus scopulorum* (USNM).

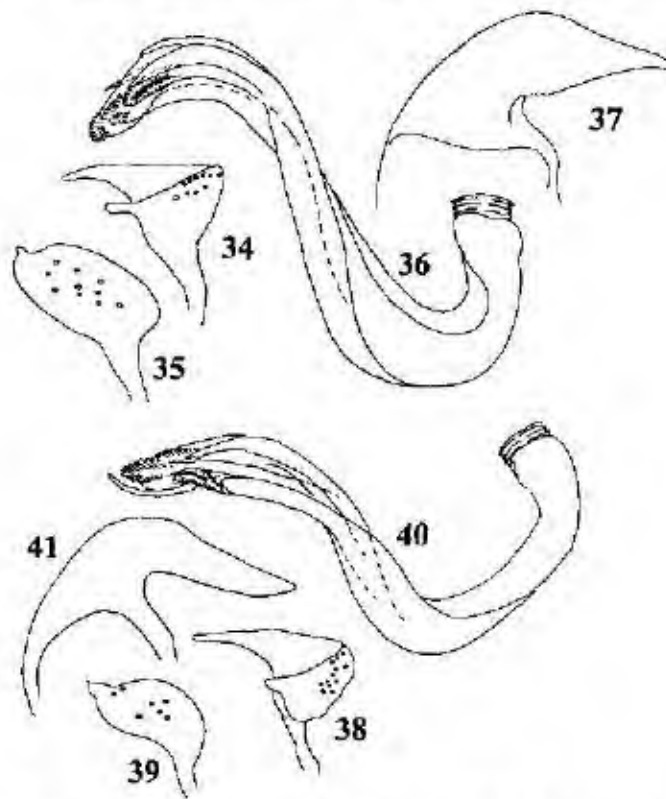
***Psallivius picetcola* (Knight, 1923) comb. n.**
(Figs 28–33, 38–41)

Psallus picetcola Knight, 1923: 469, Blatchley 1926: 959, Knight 1941: 44, Wheeler & Henry 1977: 649, Kelton 1980: 348, Wheeler et al. 1983: 138, Henry & Wheeler 1988: 494, Schuh 1995: 412.

DIAGNOSIS. This species is similar to *Psallivius flaviclavus* in overall coloration but can be separated by the longer antennal segment II that is longer than the width of the head across the eyes; from *P. rubrofemoratus* it is easily distinguished by the dark brown to fuscous, rather than reddish, femora.

DESCRIPTION. Males (n=10): Length 2.72–2.96 mm, width 1.14–1.18 mm. Head: Width 0.60–0.62 mm, vertex 0.28–0.30 mm. Rostrum: Length 1.12–1.24 mm, extending beyond metacoxae to 4th or 5th abdominal segment. Antenna: Segment I, 0.24 mm; II, 0.68–0.70 mm; III, 0.36–0.44 mm; IV, 0.26–0.32 mm. Pronotum: Length 0.44–0.46 mm, basal width 0.92–0.94.

Female (n=10): Length 2.56–2.88 mm, width 1.20–1.24 mm. Head: Width 0.60–0.62 mm, vertex 0.30–0.32 mm. Rostrum: Length 1.22–1.24 mm. Antenna: Segment I, 0.22–0.24 mm; II, 0.60–0.64 mm; III, 0.42–0.44 mm; IV, 0.28–0.32 mm. Pronotum: Length 0.44–0.46 mm, basal width 0.88–0.96 mm.



Figs 34–41. Male genitalia of *Psallivius* spp. *P. flaviclavus* (Knight), 34–37. 34 – left paramere. 35 – right paramere. 36 – vesica. 37 – phallosome. *P. picetcola* (Knight), 38–41. 38 – left paramere. 39 – right paramere. 40 – vesica. 41 – phallosome.

Tab. 1. Character matrix for *Ranzovius* processed by Hennig86

Characters	1	2	3	4	5	6	7	8	9	10	11	12	13
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Psallivius</i>													
<i>flavellavus</i>	1	0	0	1	1	0	1	0	0	0	0	1	1
<i>piceicola</i>	1	0	0	0	1	0	1	0	0	0	0	1	1
<i>rubrafemoratus</i>	1	0	0	0	1	0	1	0	0	0	0	1	1
<i>Ranzovius</i>													
<i>agelenopsis</i>	0	1	2	0	0	1	1	0	1	1	2	2	0
<i>bicolor</i>	1	1	1	1	1	1	1	0	1	1	1	2	0
<i>braulovskyi</i>	1	1	1	1	0	1	1	1	1	1	1	2	0
<i>californicus</i>	0	1	2	0	0	1	1	1	1	1	2	2	0
<i>clavicornis</i>	0	1	1	1	0	1	1	0	1	1	1	2	0
<i>crinitus</i>	0	1	1	1	0	1	1	0	1	1	1	2	0
<i>fennahi</i>	0	1	1	1	0	1	1	2	1	1	1	2	0
<i>moerens</i>	0	1	1	1	0	1	1	1	1	1	1	2	0
<i>styl</i>	0	1	1	1	0	1	1	1	1	1	1	2	0

Overall coloration dark brown to fuscous. Head (Figs 28, 29) shiny dark brown. Antenna uniformly pale yellow. Pronotum uniformly dark shiny brown to fuscous; mesoscutum and scutellum shiny dark brown; propleura with silvery scalelike setae (Fig. 33). Hemelytra dark brown, becoming somewhat paler on some specimens, apex of embolium and base and apex of cuneus pale; membrane smoky translucent brown, veins pale. Ventral surface dark brown to fuscous. Ostiolar area (Figs 31, 32) brown, anterior lobe of auricle often white. Legs: Coxae dark brown, femora dark brown with pale apices; tibiae, tarsi, and claws pale yellow.

Male genitalia: Genital capsule (Fig. 32); left paramere (Fig. 38); right paramere (Fig. 39); vesica (Fig. 40) phallosome (Fig. 41).

Hosts. Recorded from balsam fir, *Abies balsamea* (L.) Mill., Irish juniper, *Juniperus communis* L. cv. 'Hibernica', Norway spruce, *Picea abies* (L.) H. Karst; red spruce, *Picea rubens* Sarg.; white spruce, *Picea glauca* (Moench) Voss.; *Picea* spp.; and jack pine, *Pinus banksiana* Lamb. (Knight 1923, Wheeler & Henry 1977, Kelton 1980, Wheeler et al. 1983). New host records include Nordmann's fir, *Abies nordmanniana* (Steven) Spach.; Colorado spruce, *Picea pungens* Engelm.; and hemlock, *Tsuga canadensis* (L.) Carrière.

DISTRIBUTION. Known from Alberta, Illinois, Manitoba, Minnesota, New York, Pennsylvania, Quebec, Saskatchewan (Henry & Wheeler 1988), and West Virginia (Wheeler & Henry 1983). New U. S. state records are Colorado, Indiana, Iowa, Maine, Michigan, and Tennessee. Nova Scotia is a new province record for Canada.

SPECIMENS EXAMINED. **Canada: Nova Scotia:** 1 male, 3 females, Kings Co., Acadia Univ., Wolfville, 21 Jul 1994, A. G. Wheeler, Jr., on *Picea glauca* (USNM); 1 female, Kings Co., Kentville, 21 Jul 1994, A. G. Wheeler, Jr., on *Picea pungens* (USNM). **United States: Colorado:** 2 females, Redfeather Lakes, 2 Sept 1970, R. Stevens (USNM). **Indiana:** 2 females, Tippecanoe Co., West Lafayette, Purdue Univ. campus, 6 Jul 1986, T. J. Henry and A. G. Wheeler, Jr., on *Picea pungens* (USNM). **Iowa:** 3 males, 3 females, Ames, July 11, 1928, H. H. Knight (USNM); 8 males, 2 female, Ames, June 19, 1962, J. C. Schaffner, taken on *Picea pungens* (USNM). **Maine:** 1 female, Ellsworth, Sept. 4 (no other data) (USNM); 1 female, Kokadjo, Aug. 14 (no other data) (USNM). **Michigan:** 5 males, 3 females, Chippewa Co., Drummond Is., 20 July 1991, T. J. Henry and A. G. Wheeler, Jr., on *Picea glauca* (USNM); 1 female, Emmet Co., Rte 31, Pellston, 19 Jul. 1991, T. J. Henry and A. G. Wheeler, Jr., on *Picea glauca* (USNM); 3 males, Houghton Co., Michigan Tech. Univ., Houghton, 23 July 1991, T. J. Henry and A. G. Wheeler, Jr., on *Picea abies* (USNM); 3 males, Ingham Co., Danville, 15 Jul. 1991, T. J. Henry and A. G. Wheeler, Jr., on *Picea glauca* (USNM); 1 male, 2 females, Ingham Co., East Lansing, 16 July 1991, T. J. Henry

Tab. 2. Characters and character states used in analysis of the genus *Ramovius* Distant. The four left columns represent (1) character number, (2) number of steps, (3) consistency index, and (4) retention index from one (Fig. 43) of two resulting cladograms.

1.	3	33	50	Antennal segment I: dark (0), pale yellowish brown (1).
2.	1	100	100	Antennal segment I: uniformly slender (0); enlarged apically (1).
3.	2	100	100	Antennal segment II: uniformly slender throughout (0), swollen, thickness subequal to segment I (1); greatly swollen, thicker than segment I (2).
4.	2	50	75	Antennal segment II: length much greater than width of head (0); length subequal to distinctly less than width of head (1).
5.	2	50	66	Antennal segment II: dark (0), pale yellowish brown (1).
6.	1	100	100	Head length: lateral length of head anterior to eye equal to or less than the lateral width of an eye (0); lateral length of head anterior to eye distinctly greater than lateral width of an eye (1).
7.	1	100	100	Vestiture on pleuron: pleural region without sericeous setae (0); pleural region with sericeous setae in rowed pattern (1).
8.	3	66	75	Markings on cuneus: cuneus with a wide, pale mark at base (0), only apex of cuneus and embolus with pale mark (1); cuneus and embolus entirely fuscous (2).
9.	1	100	100	Metatarsal spots: spots at bases of tibial spines dark and distinct throughout (0); spots at bases of tibial spines diffused, fading distally (1).
10.	1	100	100	Length of claws: each claw long, slender, curved, much longer than diameter of tarsomeres (0); each claw short, relatively straight, length subequal to diameter of tarsomeres (1).
11.	2	100	100	Habits, species phytophagous, associated with specific host plants (0); species associated with theridid spider webs (1); species associated with agelenid spiders (2).
12.	2	100	100	Vesica shape: variable, not as in state 1 (0); sigmoid, somewhat C-shaped, with one twist, two spiculi, and a subapical secondary gonopore (1); sigmoid, somewhat C-shaped, with one twist, but with an apical gonopore (2).
13.	1	100	100	Structure of secondary gonopore on vesica: ring structure of gonopore simple (0); ring structure of gonopore with microspines or spinules (1).

and A. G. Wheeler, Jr., on *Picea abies* (USNM), 5 females, Marquette Co., No. Mich. Univ., Marquette, 25 Jul 1991. T. J. Henry and A. G. Wheeler, Jr., on *Abies concolor* (USNM); 4 males, 19 females, Mecosta Co., Ferris St. Univ., Big Rapids, 18 Jul 1991. T. J. Henry and A. G. Wheeler, Jr., on *Picea glauca* (USNM), 2 males, 7 females, Washtenaw Co., Ann Arbor, Univ. Mich., golf course, 15 Jul 1991. T. J. Henry and A. G. Wheeler, Jr., on *Picea pungens* (USNM). **Minnesota**: 8 males, 5 females (paratypes), St. Anthony Pk., 11–VII, 1922, H. H. Knight (USNM), 6 females (paratypes), Tower, Vermillion, 27 Aug. 1920, H. H. Knight (USNM). **New York**: 2 females, Ithaca, 16 Jul 1919, H. H. Knight, on spruce (USNM); 13 males, 25 females (including 6 paratypes), White Plains, VII-6-22, JRTB, taken on Norway spruce (also on hemlock and spruce) (USNM). **Pennsylvania**: 3 females, Dauphin Co., Harrisburg, E. Hbrg. Cem., 13 July 1971, A. G. Wheeler, Jr., on Norway spruce (USNM), 3 males, 2 females, Delaware Co., Haverford Coll., Haverford, 21 June 1989, A. G. Wheeler, Jr., on *Abies nordmanniana* (USNM). **Tennessee**: 4 males, 2 females, Sullivan Co., Kingsport, 26 May 1989, T. J. Henry and A. G. Wheeler, Jr., on *Picea abies* (USNM).

Psallivius rubrofemoratus (Knight, 1930) comb. n.

Psallus rubrofemoratus Knight, 1930: 129, Henry & Wheeler 1988: 495, Schuh 1995: 414.

DIAGNOSIS. This species is readily separated from *Psallivius flaviclavus* and *P. piceicola* by the bright red femora.

DESCRIPTION. Holotype male: Length 3.16 mm, width 1.20 mm. Head: Width 0.66 mm, vertex 0.28 mm. Rostrum: Length 1.14 mm, extending to bases of metacoxae. Antenna: Segment I, length 0.24 mm; II, 0.70 mm; III, 0.38 mm; IV, 0.30 mm. Pronotum: Length 0.50 mm, basal width 1.00 mm.

Overall coloration dark brown to fuscous. Head dark shiny brown. Antenna uniformly pale yellow. Pronotum, mesoscutum, and scutellum dark shiny brown to fuscous. Hemelytra brown, becoming pale yellowish brown toward base, particularly on clavus, apex of embolium and wide mark around base of cuneus pale yellow; membrane translucent brown, veins pale. Ventral surface dark brown to fuscous. Ostiolar area pale to whitish. Legs: Coxae brown with apex paler; femora red with apices pale yellow; tibiae, tarsi, and claws pale yellow.

REMARKS. This species is placed in *Psallovirus* gen. n. based on the general overall body structure, pale area around the cuneus, and the scalelike setae on the pleural areas of the thorax.

HOST. Unknown.

DISTRIBUTION. Known only from Arizona.

SPECIMEN EXAMINED. United States: Arizona: Holotype male, Mt. Lemmon, Santa Catalina Mts., July 27, 1917, H. H. Knight (USNM).

PHYLOGENETIC ANALYSIS

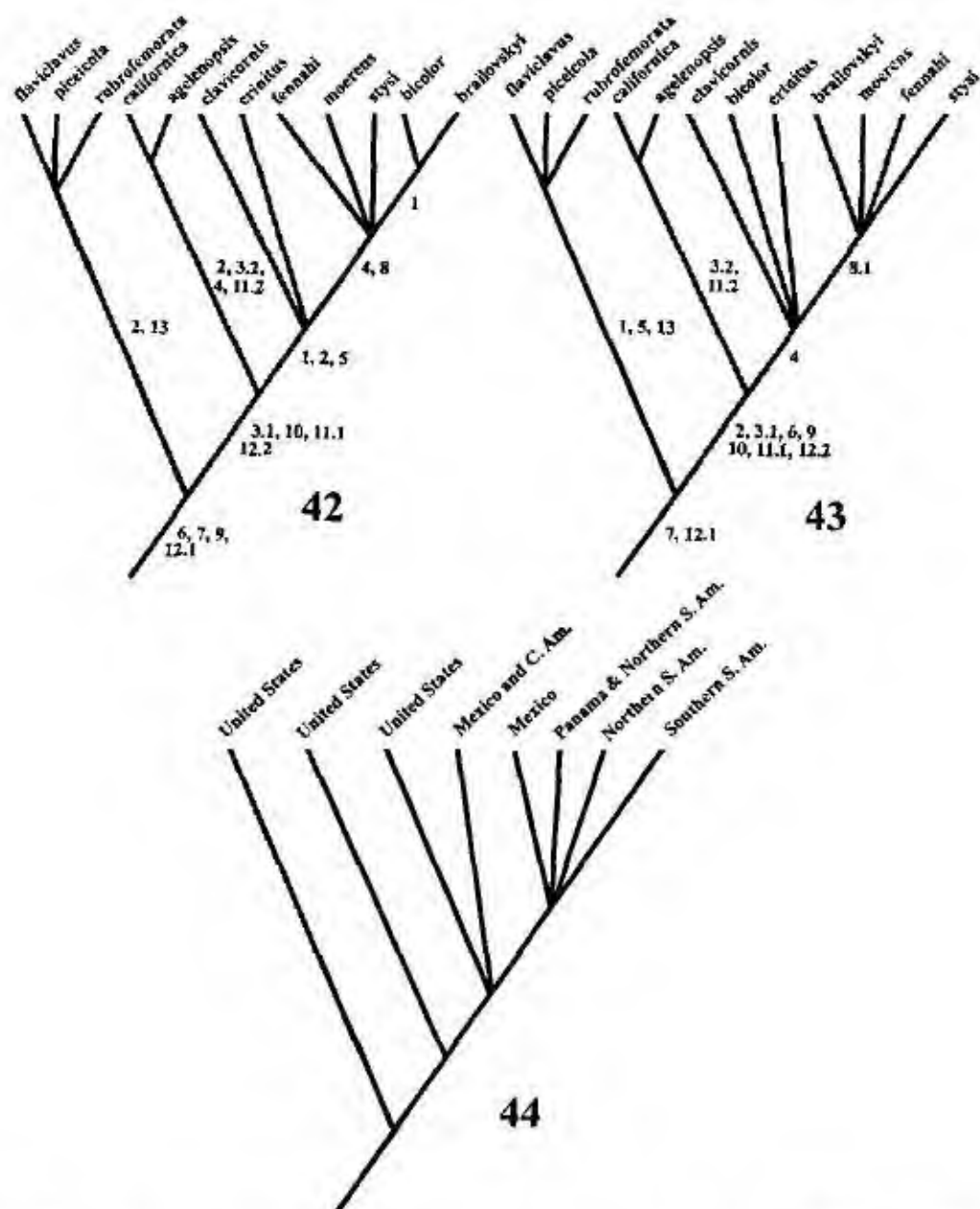
The analysis of 13 species-group taxa (Tab. 1), including 13 characters (Tab. 2) and a *mhennig* bb** search, resulted in only two cladograms (Figs 42, 43), each having a length of 20, a consistency index of 77, and a retention index of 87. Successive weighting produced only one tree, with a length of 150, a consistency of 91, and a retention index of 95. This tree is identical to one (Fig. 43) of the two trees produced by the previous *mh* bb** search. The two cladograms differ only where *Ranzovius bicolor* forms a sister-group relationship with *R. brailovskyi* in one (Fig. 42), both of which form a polychotomy with *R. fennahi*, *R. moerens*, and *R. stysi*, and where *R. bicolor* forms a polychotomy with *R. clavicornis* and *R. crinitus* in the other (Fig. 43).

This analysis supports two monophyletic genera. *Psallovirus* is hypothesized as the sister genus of *Ranzovius* in both cladograms. Together they are defined by the silvery scalelike setae on the propleural region of the thorax (character 7) and by the overall structure of the male vesica (character 12.1). *Psallovirus* is defined by pale antennal segments I and II (characters 1 & 5) and by the apical ring of the secondary gonopore having distinct microspines or spinules (character 13).

Ranzovius is defined by the swollen antennal segment I and II (characters 2 & 3), the elongate head structure (character 6), the distally fading dark spots at the bases of the tibial spines (character 9), the shorter, straighter claws (character 10), an association with spiders (character 11), and by the form of the male vesica (character 12). *Ranzovius californicus* and *R. agelenopsis* form a sister group based on their greatly thickened antennal segment II (character 3.2) and their association with agelenid spiders. The remainder of the species are poorly defined but can be grouped by the short antennal segment II that is shorter than the width of the head (character 4). The remaining species form a polychotomy, with *R. brailovskyi*, *R. fennahi*, *R. moerens*, and *R. stysi* forming a monophyletic group based on the development of pale markings around the cuneus.

BIOGEOGRAPHY

The resulting area cladogram (Fig. 44), based on a partially collapsed phylogeny of *Psallovirus* and *Ranzovius* (Fig. 43), supports an origin from a common temperate ancestor and subsequent radiation of *Ranzovius* into the Neotropics. All known members of *Psallovirus* are from the United States and Canada. The most basal clade of *Ranzovius*, *R. agelenopsis* (Tennessee) and *R. californicus* (California), is distributed in the midwestern and western United States. *Ranzovius clavicornis* (eastern North America, extending southwest to Texas and Arizona), *R. bicolor* (Mexico), and *R. crinitus* (Mexico and Central America) range from the United States into Mexico and Central



Figs 42–44 Cladograms generated by Hennig86 hypothesizing relationships of *Psallovius* genus and *Ranzovius*. Distant 42 – one of two cladograms (length 20, ci 77, ri 87) generated by mhennig* bb* functions. 43 – one of two cladograms (length 20, ci 77, ri 87) generated by mhennig* bb* functions. 44 – area cladogram based on phylogeny hypothesized in Fig. 43

America *Ranzovius braslovskyi* (Mexico), *R. moerens* (Panama and northern South America), *R. fennahi* (northern South America), and *R. shysii* (southern Brazil) form the most southerly clade, ranging south from Mexico, through Central America, to southern South America.

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Structure of the aedeagus in Miridae (Heteroptera) and its bearing to suprageneric classification

Izyslav M. KERZHNER¹⁾ & Fedor V. KONSTANTINOV²⁾

¹⁾ Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1,
St. Petersburg, RU-199034, Russia

²⁾ Department of Entomology, St. Petersburg State University, Universitetskaya nab. 7/9,
St. Petersburg RU-199034, Russia

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Abstract. A review of the structure of the aedeagus in various groups of Miridae is given. Two principal types of aedeagi are distinguished: those with eversible endosoma not subdivided into conjunctiva and vesica (Isometopinae; Cylapinae: Cylapini; Bryocorinae, except Dicyphini and some genera of Eecritotarsini; Orthotylinae: Halticini; Deraeocorinae: Teratophylini) and those with such a subdivision, the latter group includes the mirids with a vesica of Orthotylini (Orthotylinae: Orthotylini), Phylinae (Phylinae) and Mirinae type (Cylapinae: Fulvini; Bryocorinae: Dicyphini; Deraeocorinae, except Teratophylini; Mirinae). An aberrant type of vesica is found in many genera of Eecritotarsini (Bryocorinae). Functioning of aedeagus and its evolution are discussed. No changes in the suprageneric classification are formally proposed, but it is stressed that some tribes possibly deserve subfamily rank.

Morphology, evolution, classification, structure, functioning, aedeagus, Heteroptera, Miridae

INTRODUCTION

Singh-Pruthi (1925) published the first comprehensive study of the male genitalia of Hemiptera (Heteroptera and Homoptera). Among species examined by him, 5 subfamilies of Miridae were represented: Mirinae, Deraeocorinae (both under the name Capsinae in Singh-Pruthi), Bryocorinae (as Bryocorinae and Dicyphinae), Orthotylinae (Cyllocorinae) and Phylinae (Plagiognathinae). Singh-Pruthi (1925) noticed that in Bryocorinae (*Monalocoris* and two genera of Dicyphini examined) the aedeagus is without vesica, whereas in all other examined families a vesica is present. The absence or presence of vesica was considered by Singh-Pruthi (1925) a very important character, and all Heteroptera were divided by him (Singh-Pruthi 1925: 237) in respective two groups: «families with Reduviid type of genitalia» (without a vesica) and «families with Pentatomid type of genitalia» (with a vesica). Singh-Pruthi (1925) indicated that the vesica of Miridae differs from that in pentatomomorph families, and that the Miridae are undoubtedly related to cimicomorph families (Tingidae, Reduviidae, etc.).

Kullenberg (1941, 1947) described in detail the male and female genitalia and copulation in common Swedish species of Miridae and Nabidae. His study, though extremely careful and containing many important conclusions, does not discuss the higher classification of Miridae. The subfamilies examined by him were the same as in Singh-Pruthi's study. Kullenberg correctly noted that in Bryocorini (*Bryocoris* and *Monalocoris* examined) the vesica is absent, but in Dicyphini it is present.

Carvalho & Leston (1952) stated that «there appear to be four main types of aedeagus in the family, Deraeocorinae (common to Cylapinae also), Bryocorinae, Phylinae (common to Orthoty-

linae also) and Mirinine». They did not indicate any characters of these types, and our study does not support this classification.

Dupuis (1955) published an extensive review of information on the genitalia of Heteroptera. He followed (Dupuis 1955: 200–201) Singh-Pruthi in dividing Miridae into two principal groups based on the absence or presence of vesica. In the first group he placed Bryocorinae and Dicyphinae (now both united in Bryocorinae). He indicated that further subdivisions, already suggested by Wagner (1952), can be made in the group with a vesica, based on the degree of its sclerotization («type Mirinae» and «type Phylinae»).

Some examples of the use of the aedeagus structure for distinguishing closely related species of Miridae can be noted in the 20's and 30's (e. g., Knight 1923). E. Wagner was the first author who widely used the structure of the aedeagus for separation of related species and in some cases for delimitation of genera and suprageneric taxa. Wagner (1952) distinguished two types of structure of aedeagus (Mirinae and Phylinae types) to which he later (Wagner 1955) added a third one (Orthotylinae type). Wagner did not recognize mirids without vesica as a separate group and included them in the «Mirinae type» (see e. g., Wagner & Weber 1964: 14: «Le type Mirinae se trouve chez les Mirinae, les Deracocorinae, les Cylapinae, les Dicyphinae, les Bryocorinae, les Halticini et même chez les Isometopidae»).

Kelton (1955, 1959) used the male genitalia for subdivision of the *Lygus* Hahn, 1833 complex into genera and subgenera and published a richly illustrated review of the male genitalia in many genera of Holarctic Miridae. He used the term vesica for various structures inside the theca: the true vesica, combination of vesica and conjunctiva, and undivided endosoma.

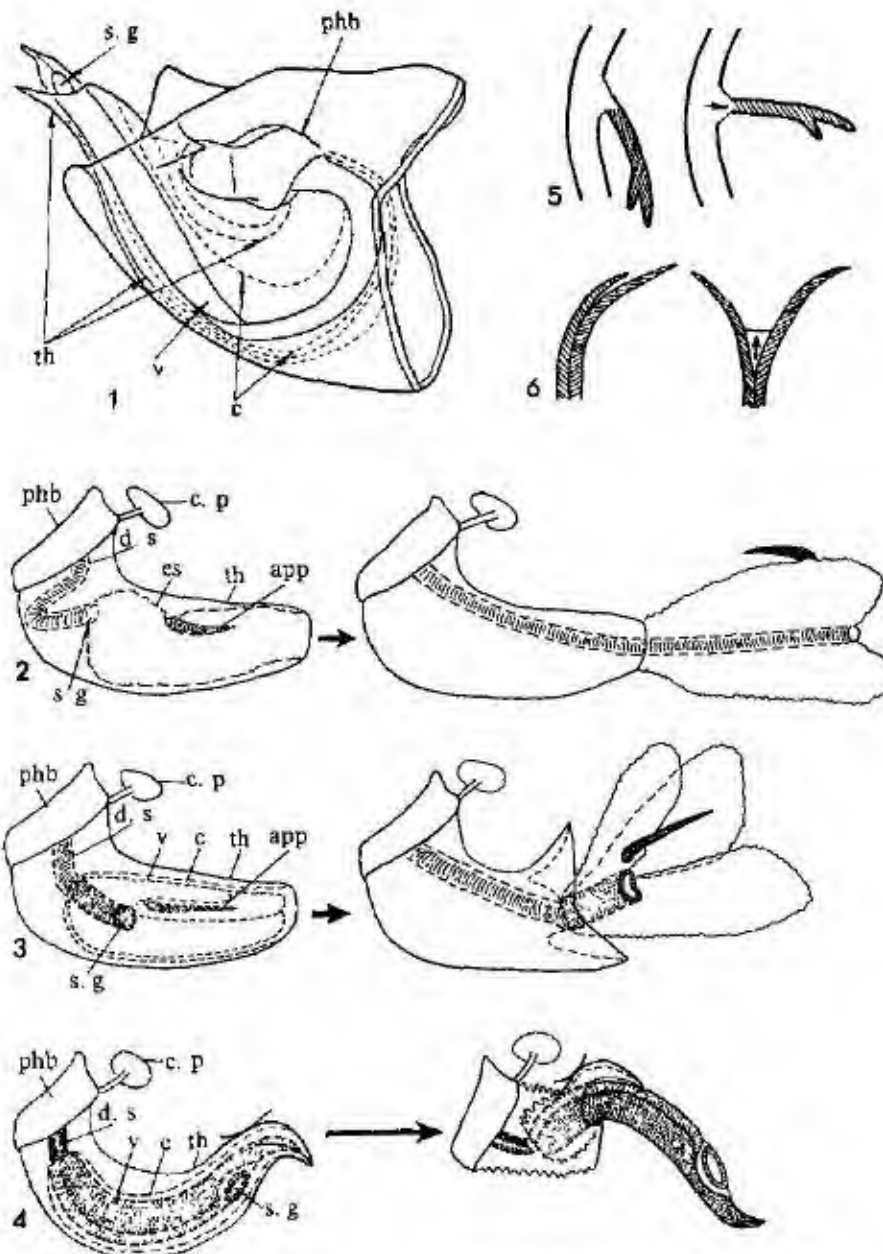
In the second half of the XXth century, examination and illustration of aedeagi became an integral part of practically all taxonomic publications on Miridae. Numerous figures of aedeagi (mostly of vesicae or their sclerotized appendages) were published by A. Carapezza, J. C. M. Carvalho, T. J. Henry, M. V. Josifov, L. A. Kelton, I. M. Kerzhner, H. H. Knight, R. E. Linnavuori, T. R. Odhiambo, J. Ribes, J. C. Schaffner, R. T. Schuh, M. D. Schwartz, G. Seidenstücker, G. M. Stone-dahl, L. Tamarin, E. Wagner, T. Yasunaga, L. Y. Zheng, and many other authors.

Since the second half of the XIXth century (Thomson 1871, Reuter 1875, 1910, Carvalho 1952, Schuh 1976) the subfamily classification of Miridae is based mainly on the structure of pretarsus combined with some other external characters (presence or absence of pronotal collar, venation of membrane, etc.). In the last decades, the structure of aedeagus was used to refine the systematic position of many genera and some tribes (e. g., Pilophorini), but in groups not having a true vesica the structure of aedeagus was usually misinterpreted and neglected in discussions on phylogeny and classification.

MATERIAL AND METHODS

This study is based on examination of a limited number of genera representing all subfamilies, except for Psalloppiinae and Palaeocorinae. Dry specimens from the collection of the Zoological Institute, St. Petersburg, including some copulating pairs, were used. Some specimens of Cylapinae were received from Dr R. T. Schuh.

The methods of extracting the vesica in Deracocorinae (except for Termatophylini), Mirinae, and Phylinae are well known to taxonomists and described in many monographs and special publications (e. g., Clayton 1989). In these three groups to which most of the Holarctic mirids belong, the conjunctiva connecting the vesica with the theca and in Phylinae also the basal part of the theca are membranous, very thin, easily ruptured in process of extraction of vesica from theca (or from its apical part) and mostly even not noticed. From another hand, the proximal part of ductus seminis in these groups is short and stout, and not ruptured when the theca (or its sclerotized apical part) and phallobase are pulled with pins in opposite directions. The sclerotized vesica of Phylinae is non-inflatable. The membranous vesicae of Deracocorinae and Mirinae should be treated in solution of KOH or NaOH and then placed in distilled water for inflation; because of differences in osmotic pressure, the membranous sacs become inflated.



Figs 1-6 Aedeagi of Miridae 1 - *Psallus ambiguus* Fallén, schematical representation of the male genital segment with aedeagus in repose (after Kullenberg, 1947); 2-4 - aedeagus in repose (left) and erected (right), schematically (2 - not having vesica; 3 - with vesica of Mirinac type; 4 - with vesica of Phyllinac type), 5-6 - anchoring elements of vesica in repose (left) and in erected aedeagus (right), schematically (5 - some Pilophorini, e. g., *Pilophorus* Hahn; 6 - some Phyllini, e. g., *Plagiognathus* Fieber).

In Fulvini, Diegphini and those Eecentotarsini which have a vesica, the extraction of the vesica from the theca is more difficult because the soft-walled and long proximal part of the ductus seminis is easily ruptured and the conjunctiva is thicker than in Mirinae and Deracocornae, in addition, the specimens, and their genitalia, are very small. Sometimes it is possible at least partially to pull out the vesica after treatment in KOH or NaOH with accurate manipulations using micropins. Another possibility is to separate the theca from the phallobase, and using pins, tear the theca away part by part, when most of it torn away, it is necessary to move the conjunctiva (and remainder of the theca) towards the phallobase, as a result of this operation, the vesica becomes free and can be inflated as in Mirinae. In the Orthotylini, the sclerotized elements important for species identification are placed on the proximal part of conjunctiva, around the «simple» vesica. After separation of the theca from the phallobase, it is necessary, acting accurately with pins, to tear away the theca with the distal parts of the thin transparent conjunctiva, then the vesica and surrounding sclerotized processes can be illustrated. In some species with a weakly sclerotized theca, the sclerotized processes can be drawn as they are seen through the transparent theca.

In the groups not having a vesica, the methods of examination and illustration of the aedeagus may be different, similar to those used for examination of the aedeagi of Nabidae. In repose, the long ductus seminis and the membranous endosoma are usually bent, coiled and folded within the theca and difficult to see and illustrate even when the theca is more or less transparent. After separation of the theca from the phallobase, sometimes it is necessary to break off the proximal part of the theca covering the internal sclerotized elements. In some species it is possible to pull out most of the inner part of the aedeagus through a longitudinal slit of the theca (Fig. 19). Successive treatment with solution of KOH or NaOH and water helps to inflate the membranous folds. The aedeagus should be drawn with sclerotized elements and other armament inside. In some works (especially on Hattierini), the sclerotized elements of aedeagus are extracted and drawn separately, but in that case the information on their position on the endosoma is lost.

The following abbreviations are used in the figures: app, sclerotized appendage, c, conjunctiva, c p, capitae process, d s, ductus seminis, es, endosoma, p g s, internal process of genital segment, phb, phallobase, s g, secondary gonopore, sp, spicula, th, theca, th m, theca mouth, v, vesica. All scale bars equal 0.05 mm.

Terminology

The terminology of aedeagal structures is confused by the use of numerous synonyms and misuses. A brief explanation of the terms used in this work is given below.

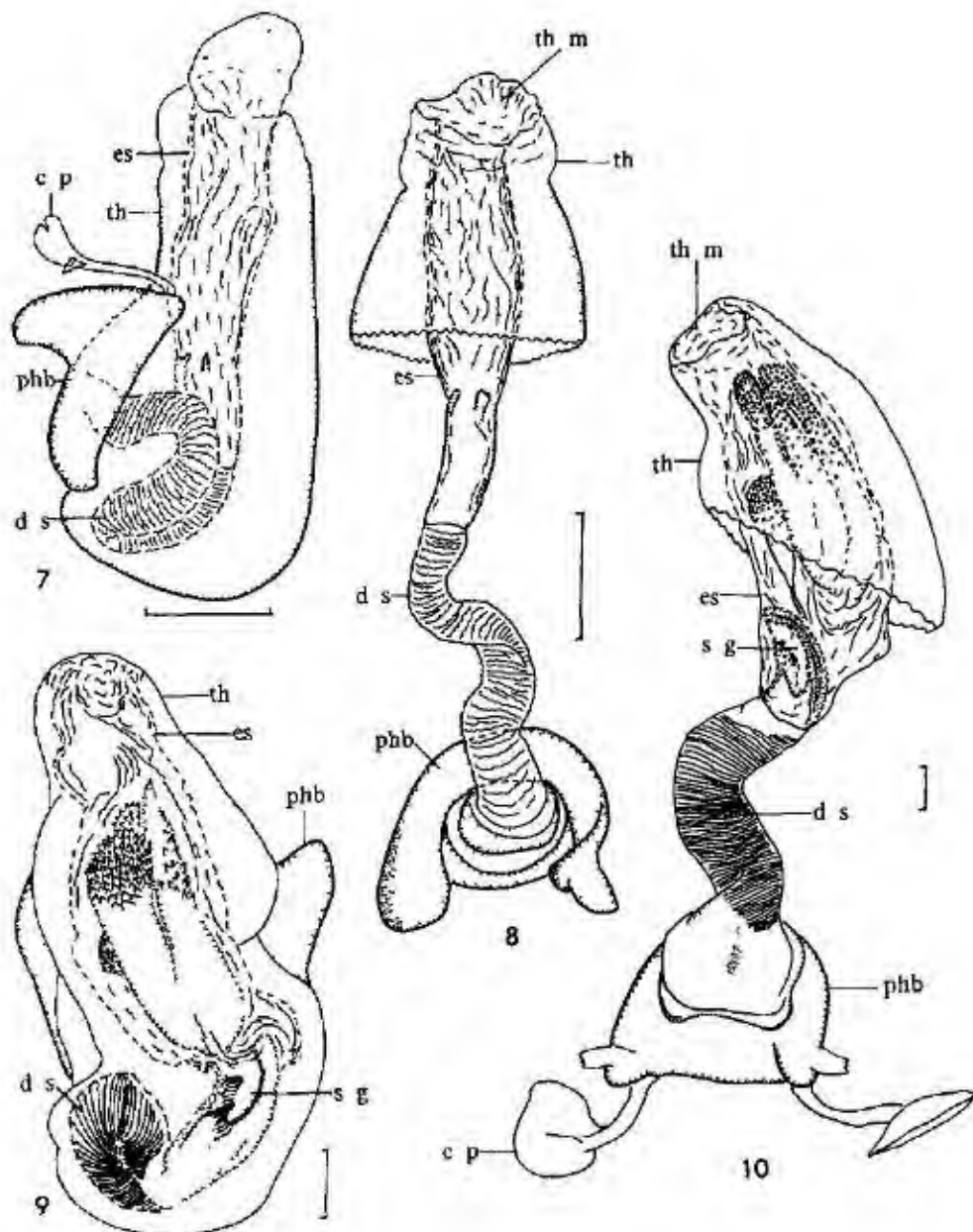
Aedeagus (penis, phallus) is the organ for sperm intromission. From its origin, it is a two-walled tube-like projection of the membranous intersegmental diaphragma between abdominal segments IX and X around the opening (primary gonopore) of the mesodermal ductus ejaculatorius. The term phallus is often used in the literature for the aedeagus plus the phallobase.

Phallobase (basal plates in Singh-Pruthi 1925, basal articulatory apparatus in Schuh & Slater 1995) is formed by two plates surrounding the base of aedeagus. They form a horseshoe-shaped swelling of the diaphragma with lateral arms connected by a bridge. With a few exceptions (e.g., *Mecommopsis* Kerzhner, 1979 in the Orthotylini), the phallobase is symmetrical. Its dorsolateral corners are prolonged into two mushroom-like capitae processes (reduced in Bryocorini). Protractor and retractor muscles are fastened both to the phallobase and to the capitae processes (for details, see Kullenberg 1947). When the male genitalia are dissected, the thin intersegmental membrane around phallobase is ruptured and the phallobase is separated together with the aedeagus.

Theca (phalotheca, phallosoma) is the external part of the aedeagus viewed in repose. It is more or less tube-like, usually elongate and narrowing distad, with apex usually sticking out from the opening of the genital segment in repose, with a slit-like, round or oval apical or subapical opening. Usually the theca is moderately sclerotized, sometimes it is provided with one or few projections, teeth, or keels in the area adjacent to the opening. In some groups the theca has areas of weaker sclerotization at the base or on the ventral side (on the peculiar structure of the theca in Phylinae see below). During copulation, the apex of the theca is placed opposite the female vulva (entrance in the bursa copulatrix) or inserted into it.

Endosoma is the internal (in repose) part of aedeagus between the opening of the theca and the secondary gonopore. It is more or less tube-like, membranous, sometimes with sclerotized structures on the inner side. In mirids without a vesica, the endosoma is everted from the theca during the copulation and inserted into the bursa copulatrix (vagina) of the female. When mentioning proximal and distal parts of the endosoma, we have in mind their position in repose.

In most mirids, the endosoma is subdivided into two parts: the outer (conjunctiva) and the inner (vesica). The conjunctiva in all groups, except Orthotylinae (and one genus of Mirinae), is devoid of sclerotized structures. It is eversible and connects the theca with the vesica. The vesica is formed by the proximal part of the endosoma which envelopes the distal section of the ductus seminis and is fused with it at the base of this section. During copulation, the vesica is not everted. It is either membranous or (in Phylinae) nearly entirely sclerotized.



Figs 7-10: Aedeagi of Isometopinae (7-8) and Cylapini (9-10). 7-8 - *Isometopus kaznakovi* Kuritsshenko (7 - aedeagus in repose, lateral view, 8 - aedeagus with proximal part of theca detached), 9 - *Cylapus ruficeps* Bergroth, aedeagus in repose, ventral view, 10 - *C. citus* Bergroth, aedeagus with proximal part of theca detached.

Ductus seminis is a tube inside of aedeagus for transfer of the sperm. Its inner wall, at least in some areas, is strengthened with sclerotized rings (see Kullenberg, 1947: 394, figs 24-26, for details). The distal end of the ductus seminis passes directly into the endosoma in the mirids without a vesica. In the mirids with a vesica, the distal part of ductus seminis is inside of vesica.

Primary gonopore is an opening (foramen) in the intersegmental diaphragma about in the centre of the phallobase. Through this opening the mesodermal ductus ejaculatorius, bringing the sperm from the testes, is connected with the ectodermal ductus seminis lying inside of aedeagus.

Secondary gonopore is an opening at the distal end of ductus seminis through which the sperm is ejaculated into the female. Usually it is surrounded by a ring with characteristic sculpture.

RESULTS

Structure of the aedeagus in various groups of Miridae

1. Isometopinae (*Isometopus kaznakovi* Kiritshenko, 1939 examined; see also Akingbohunge 1996). Figs 7, 8. Capitae processes weakly developed. Theca weakly sclerotized. Vesica absent. Ductus seminis partly sclerotized and without rings in its distal part; secondary gonopore without especial structures. Endosoma without sclerotized structures.

2. Cylapinae. Of the three tribes distinguished by Carvalho (1952), Bothriomirini were not examined.

2.1. Cylapini (*Cylapus ruficeps* Bergroth, 1922 and *C. citus* Bergroth, 1922 examined). Figs 9, 10. Theca weakly sclerotized, except its dorso-proximal area. Vesica absent. Ductus seminis not sclerotized, flexible; secondary gonopore distinct, with characteristic sculpture. Endosoma on inner side with four sclerotized processes covered apically with small denticles.

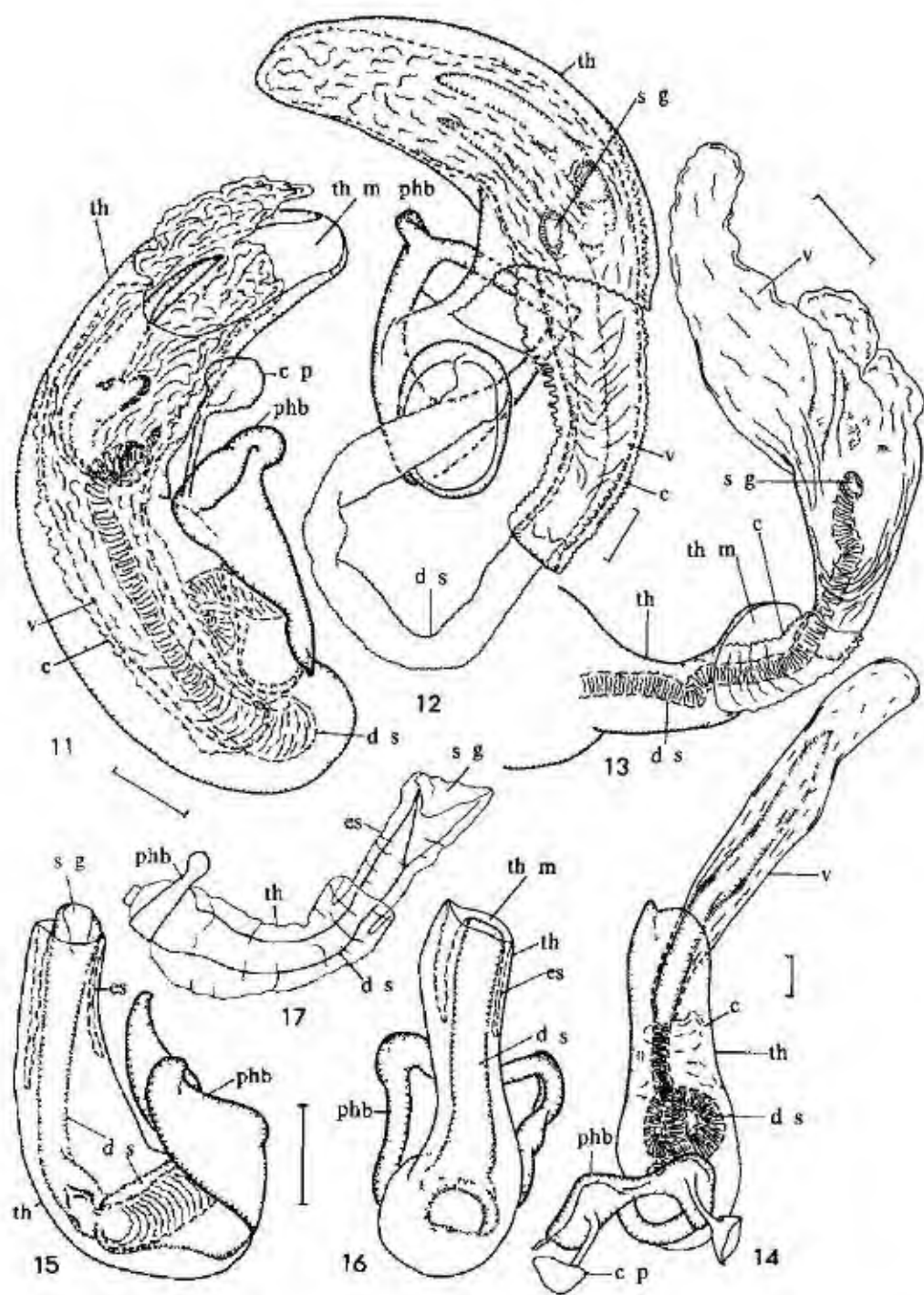
2.2. Fulvini (*Fulvius* Stål, 1862, *Punctifulvius* Schmitz, 1978 and *Rhinocylapidius* Poppius, 1915 examined; a similar structure of aedeagus is described for other genera, e. g., *Carvalhofulvius* Stonedahl et Kovac, 1995, see Stonedahl & Kovac 1995). Figs 11-14. Theca moderately sclerotized. Vesica present. The part of ductus seminis lying outside the vesica relatively long. Conjunctiva devoid of sclerotized structures but less thin compared to that of Deraeocorinae or Mirinae. Vesica of Mirinae type, with inflatable membranous lobes and sometimes with sclerotized armament. In *Fulvius* and *Punctifulvius* (Figs 11-13), ductus seminis within the vesica not sclerotized, with rings, secondary gonopore less distinct than in Mirinae and Deraeocorinae. In *Rhinocylapidius* (Fig. 14), ductus seminis within the vesica sclerotized, spine-like, secondary gonopore invisible. In all examined genera, ductus seminis not forming a reservoir at base of vesica.

3. Bryocorinae. Representatives of all tribes were examined.

3.1. Bryocorini (*Bryocoris* Fallén, 1829 and *Monalocoris* Dahlbom, 1851 examined). Figs 15-17. Capitae processes reduced. Theca weakly sclerotized. Vesica absent. Proximal third of ductus seminis with rings, strongly swollen and sclerotized at base, but becoming narrower and less sclerotized distad. Distal two-thirds of ductus seminis placed at an angle to the proximal third, sclerotized (except, at least partly, the ventral side), reaching in repose the apex of theca. Endosoma devoid of sclerotized structures.

3.2. Monalonini (*Dimia* Kerzhner, 1988 and *Monalonion* Herrich-Schaeffer, 1850 examined) and Odoniellini (*Odoniella* Haglund, 1895 examined). Fig. 18. Theca sclerotized at dorsal side only. Ductus seminis long, coiled, with rings. Vesica absent. Endosoma with sclerotized armament.

Figs 11-17. Aedeagi of Fulvini (11-14) and Bryocorini (15-17). 11-13 - *Punctifulvius kerzhneri* Schmitz (11 - aedeagus in repose, lateral view; 12 - aedeagus in repose with theca separated from phallobase, 13 - apex of erected aedeagus); 14 - *Rhinocylapidius* sp. (Malaya), erected aedeagus, dorsal view; 15-17 - *Bryocoris pteridis* Fallén (15 - aedeagus in repose, lateral view; 16 - aedeagus in repose, ventral view; 17 - erected aedeagus, lateral view, after Kullenberg 1947).



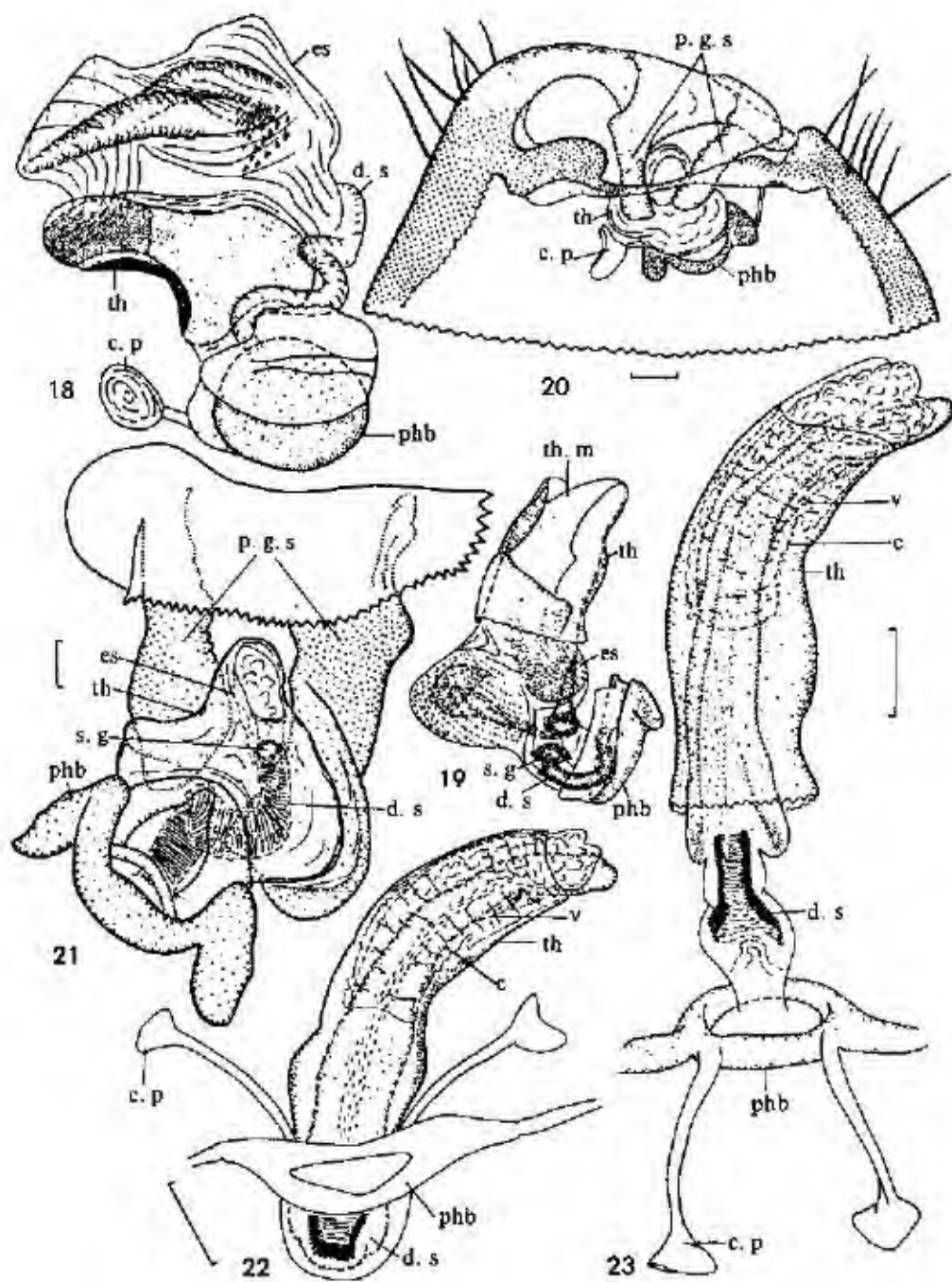
3.3. *Eccritotarsini* (10 genera examined). Figs 19–29. The structure of aedeagus is variable. In *Sinevia* Kerzhner, 1988 (Fig. 19) and *Michailocoris* Štys, 1985 the endosoma is not subdivided into a conjunctiva and vesica, has sclerotized armament, and the structure of aedeagus is similar to that of Monalonini and Odoniellini. In *Pycnoderes* Guérin-Ménéville, 1857 (Figs 20, 21) and *Sixeonotus* Reuter, 1876, the genital segment is provided, on inner ventral side, with two internal processes supporting the aedeagus; theca weakly sclerotized; endosoma not subdivided into conjunctiva and vesica, small, without sclerotized armament; secondary gonopore distinct, with characteristic sculpture. In *Parafurius* Carvalho et China, 1951, *Heterocoris* Guérin-Ménéville, 1857 (Fig. 29), *Eurycipitia* Reuter, 1905 (Fig. 27), *Neella* Reuter, 1908 (Fig. 28), *Eccritotarsus* Stål, 1860 (Figs 21–23) and *Cyrtocapsus* Reuter, 1876 (Figs 24–26), the vesica is uniquely developed: the distal portion of the ductus seminis is strongly sclerotized, usually spine-like and reaching the apex of the theca in repose; apparently, the membranous part of vesica is partly fused with the distal portion of ductus seminis and partly (except *Cyrtocapsus*) forming a membranous lobe; conjunctiva thin and without armament. Conjunctiva is apparently connected to the middle part of the sclerotized portion of ductus seminis in *Eccritotarsus*, and near to its base in other genera; in *Cyrtocapsus*, the membranous lobe is absent and the vesical membrane apparently entirely fused with the sclerotized part of ductus seminis. The opening of the secondary gonopore in the above genera is apical and very small. The proximal, membranous part of ductus seminis is placed in a weakly sclerotized sac-like projection of the theca which is probably rumpled during the copulation; this projection is especially large in *Cyrtocapsus*.

3.4. *Dicyphini* (*Dicyphus* Fieber, 1858, *Cyrtopeltis* Fieber, 1860, *Nesidiocoris* Kirkaldy, 1902 and *Macrolophus* Fieber, 1858 examined). Figs 30–36. Theca sclerotized dorsally and membranous ventrally. Vesica present (but see below on *Cyrtopeltis geniculata* Fieber, 1861), with inflatable folded lobes and sometimes with sclerotized armament. Ductus seminis outside the vesica weakly sclerotized, long, with rings. Kullenberg (1947) stated that in *Dicyphus* the secondary gonopore is placed between arms of the horseshoe-shaped sclerite at base of vesica, but we observed a hardly visible continuation of ductus seminis, with very thin walls, reaching to about the middle of the non-erected vesica and sometimes terminating with an indistinct ring of minute transparent tubercles on the surrounding vesical lobes. In *Cyrtopeltis*, there is a small movable sclerite at the distal end of ductus seminis. It seems that in *C. rufobrunnea* Lee et Kerzhner, 1995 there is a true vesica fastened to this sclerite, but in *C. geniculata* the non-eversible central lobe covered with minute teeth seems to be not a true vesica, but one of the membranous lobes of endosoma. The ductus seminis in both species opens at the above-mentioned sclerite. *Nesidiocoris* and *Macrolophus* have a vesica but the sclerite at its base is absent. In *Nesidiocoris*, ductus seminis inside of vesica distinct, with rings, its distal portion sclerotized. In *Macrolophus*, ductus seminis inside of vesica hardly visible.

4. *Orthotylinae*. Of the three tribes included in this subfamily, *Nichomachini* are not examined by us.

4.1. *Halticini* (*Halticus* Hahn, 1832, *Labops* Burmeister, 1835, *Strongylocoris* Blanchard, 1840, *Myrmecophyes* Fieber, 1870 and *Orthocephalus* Fieber, 1858 examined). Figs 37–39. Theca moderately (in *Halticus* strongly) sclerotized, with less sclerotized ventro-proximal part; opening of theca apical, slit-like in repose. Vesica absent. Ductus seminis divided into long, flexible proximal part of

Figs 18–23. Aedeagi of Monalonini (18) and Eccritotarsini (19–23). 18 – *Dinia inexpectata* Kerzhner, aedeagus with theca partly detached and endosoma taken out through a ventral slit (after Kerzhner 1988); 19 – *Sinevia tricolor* Kerzhner, aedeagus with theca ruptured in proximal part, lateral view (after Kerzhner 1988); 20–21 – *Pycnoderes* sp. (20 – apex of genital segment with dorsal side removed and aedeagus in repose, dorsal view; 21 – processes of genital segment and aedeagus in repose, ventral view); 22–23 – *Eccritotarsus* sp. (22 – aedeagus in repose, dorsal view; 23 – aedeagus with theca separated from phallobase)



usual structure and shorter, sclerotized distal portion bearing the secondary gonopore in latero-apical position; margin of secondary gonopore with characteristic sculpture. Endosoma with various sclerotized structures (spiculae, spines, fields of sclerotized tubercles, etc.) which are often placed in eversible membranous sacs.

4.2. Orthotylini (*Orthotylus* Fieber, 1858, *Blepharidopterus* Kolenati, 1845, *Cyllecoris* Hahn, 1834 and *Heterocordylus* Fieber, 1858 examined). Figs 40, 41. Theca moderately sclerotized, with a large oval opening, either apical or dorso-subapical, in the latter case the conjunctiva is connected with the theca far from its apex, at the level of the proximal margin of the opening. Orthotylini have a «simple» vesica. It is formed by the sclerotized distal portion of ductus seminis surrounded by a thin membranous proximal portion of endosoma. Secondary gonopore ventro-subapical. The membrane of vesica without sclerotized or inflatable appendages. The remaining part of the endosoma, the membranous conjunctiva, is not very thin. The part of the conjunctiva adjacent to the vesica usually with long sclerotized processes connected at base, variously branched and often toothed at margins. In inflated aedeagus, some of these processes occupy a perpendicular position to vesica, apparently acting as an anchor in the bursa copulatrix of the female. However, in some Orthotylini (*Blepharidopterus*, some species of *Orthotylus*) these processes are small and not branched, and in some (*Ceratocapsus* Reuter, 1876) they are lacking (Kelton 1959).

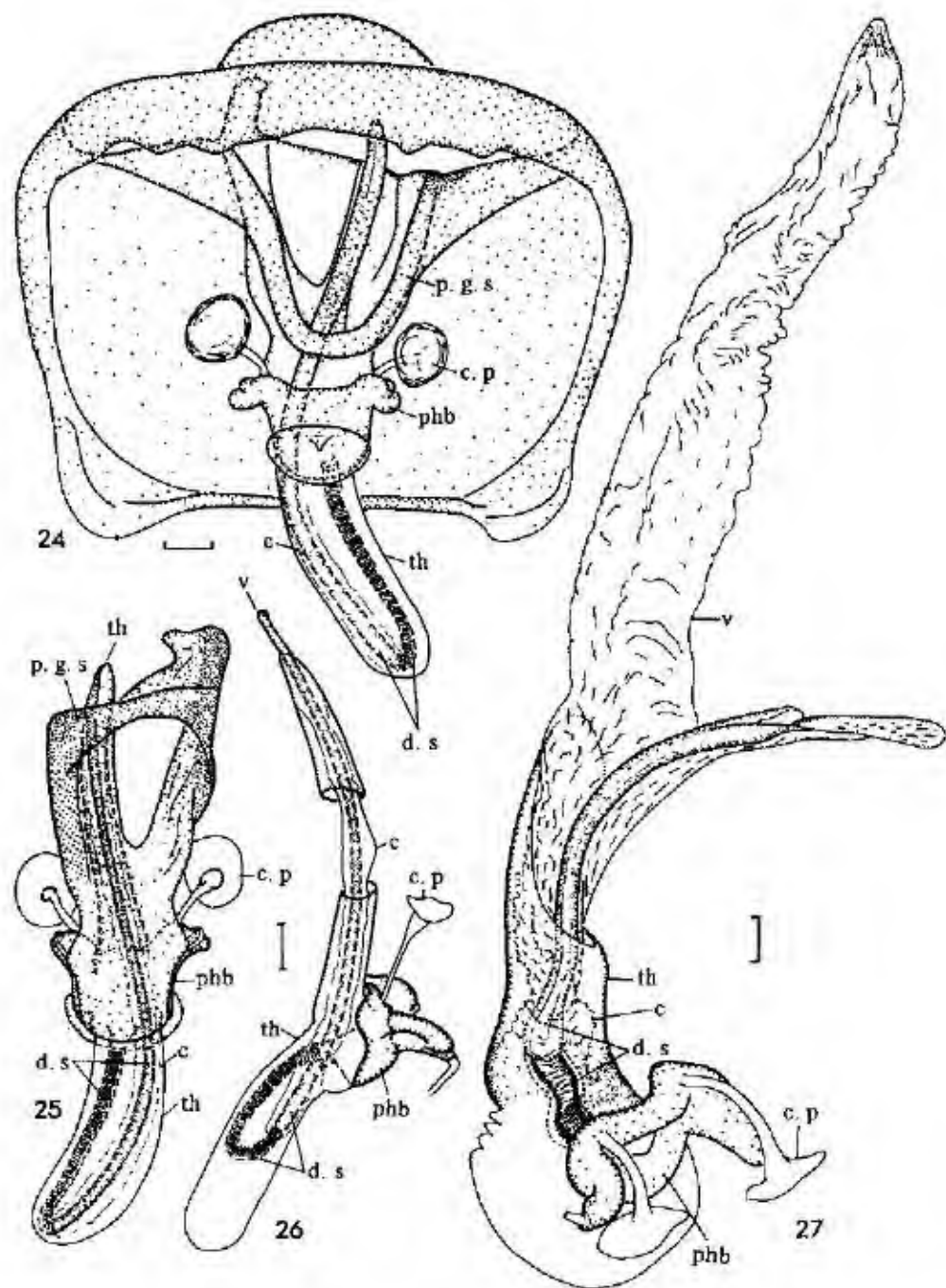
5. Phylinae (many genera examined). Figs 42–44. Theca with proximal part membranous, with very thin walls; its distal part strongly sclerotized, in form of a curved conus immovably connected at base with the ventral wall of the male genital segment, with a slit-like latero-apical opening. Conjunctiva very thin, without armament. Vesica long, strongly sclerotized, usually C-form or S-form, formed by a sclerotized gutter covered by a membranous wall. However, in Pilophorini and some genera of Phylini the main part of vesica is round in cross-section and entirely sclerotized. The part of ductus seminis lying outside of vesica is solid and short; the part running inside of vesica is thin-walled and difficult to observe. Secondary gonopore placed in the apical third of vesica, sometimes apically, often surrounded by a ring with characteristic sculpture. Its opening is very small in many Pilophorini.

6. Deraeocorinae. Representatives of two tribes (Saturniimirini and Surinamellini) were not examined, but judging from the published figures their aedeagi are similar to those of most Deraeocorinae.

6.1. Termatophylini (*Argyrotelaenus* Reuter et Poppius, 1912, *Termatophylum* Reuter, 1884 and *Kundaktimuka* Cassis, 1995 examined; for other genera see Cassis 1995). Figs 45–47. Structure of aedeagus strongly different from that of other Deraeocorinae. Theca weakly sclerotized, but with a sclerotized dorso-proximal stripe prolonged distad along lateral margins. Vesica absent. Ductus seminis long, coiled, with distinct rings on inner wall. Secondary gonopore hardly visible, with two small sclerites. Endosoma voluminous, folded, with fields of sclerotized microstructures and sclerotized appendages. Judging from the work of Cassis (1995), the endosoma of *Termatophylidea* Reuter et Poppius, 1912 is aberrant, «with a sclerotized process, directly connected to the termination of the ductus seminis, and almost reaching apex of vesica [i. e. distal margin of endosoma – I. K. & F. K.]», without sclerites or fields of spines.

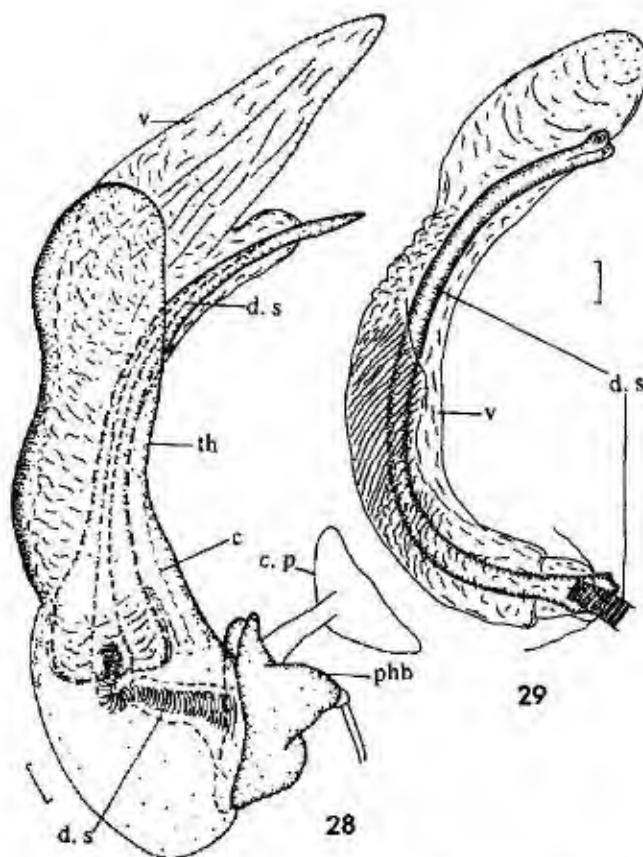
6.2. Deraeocorini (*Alloeotomus* Fieber, 1858 and *Deraeocoris* Kirschbaum, 1856 examined), Clivinematini (*Bothynotus* Fieber, 1864 examined) and Hyaliadini (*Hyaliodes* Reuter, 1876 and *Stethocornus* Flor, 1861 examined). Fig. 48. These tribes have aedeagal structure resembling that of Mirinae. Theca more or less uniformly sclerotized, narrowed to apex. Vesica as in Mirinae, with inflatable

Figs 24–27. Aedeagi of Ecentotarsini. 24–26 – *Cyrtocapsus* sp. (24 – apex of genital segment with aedeagus in repose, dorsal view; 25 – processes of genital segment and aedeagus in repose, ventral view; 26 – aedeagus with theca ruptured in distal third), 27 – *Eurycipitia clara* Distant, erected aedeagus



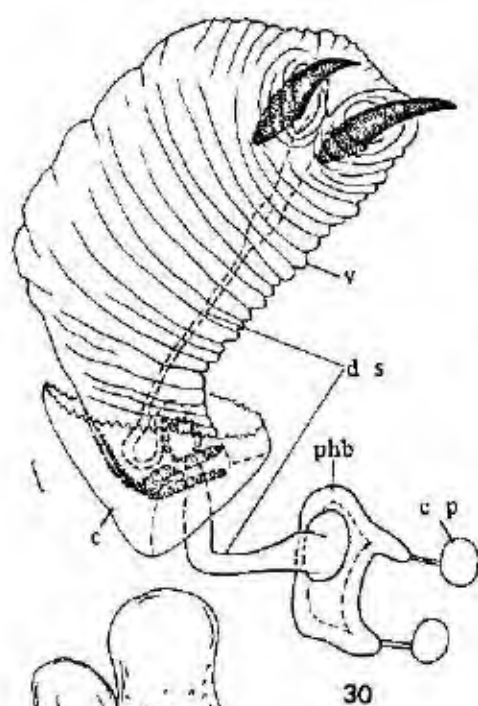
membranous lobes and sometimes with sclerotized appendages, but ductus seminis moderately sclerotized, without reservoir, and secondary gonopore less distinct than in Mirinae. Conjunctiva very thin.

7. Mirinae (many genera of various tribes examined). Figs 49–50. Theca more or less uniformly sclerotized, narrowed towards apex, with a subapical or apical slit-like opening. Vesica with several inflatable membranous lobes, often with one or several sclerotized appendages, particularly with long and thin processes termed spiculae, sometimes with combs or fields of teeth. The section of ductus seminis outside the vesica relatively short, flexible, with sclerotized rings, the section inside the vesica markedly sclerotized and often with a widened area (reservoir). Secondary gonopore distinct, lip-like. Conjunctiva very thin and without armament, except for *Capsus* Fabricius, 1803

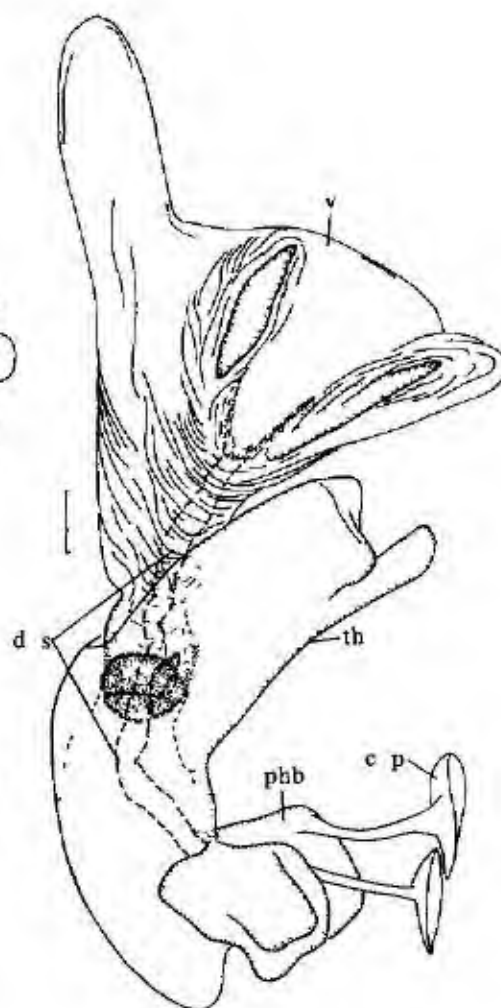


Figs 28–29. Aedeagi of Ecritotarsini. 28 – *Neella explanata* Carvalho, moderately erected aedeagus, lateral view; 29 – *Heterocoris cyaneus* Knight, vesica.

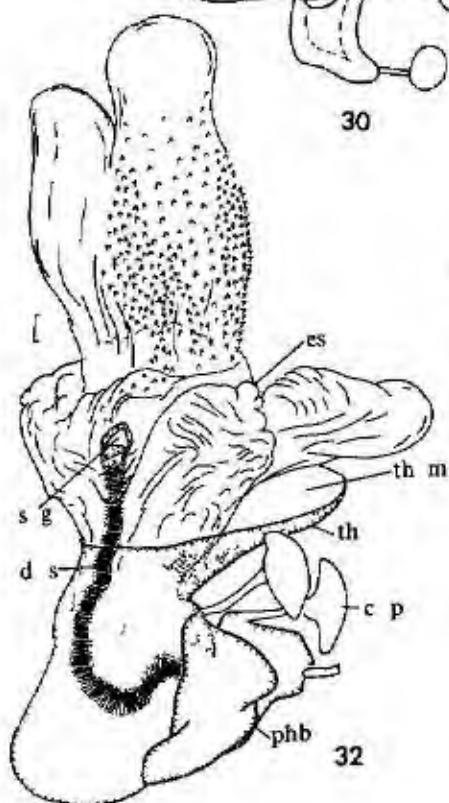
Figs 30–32. Aedeagi of Dicyphini. 30 – *Dicyphus errans* Wolff, erected aedeagus with theca and part of conjunctiva removed, 31 – *D. constrictus* Boheman, erected aedeagus; 32 – *Cyrtopeltis geniculata* Fieber, erected aedeagus.



30



31



32

(Fig. 50) in which conjunctiva bears in the area adjacent to vesica a long curved spicula with base embedded in a membranous sac

Summarizing the above review we may accept the following categorization of the aedeagus structure

A Aedeagus without vesica Isometopinae, Cylapini, many Bryocorinae, Teratophylini, Halticini

B Aedeagus with vesica

B1 Vesica of Orthotylini type (without inflatable lobes and sclerotized armament, the latter placed on conjunctiva) Orthotylini

B2 Vesica of Phylinae type (strongly sclerotized) Phylinae

B3 Vesica of Mirinae type (with inflatable membranous lobes) Fulvini, Dicyphini, Deraeocorinae (except Teratophylini), Mirinae

Some genera of Eccritotarsini have a vesica of especial type sharing certain peculiarities with the subtypes B2 and B3

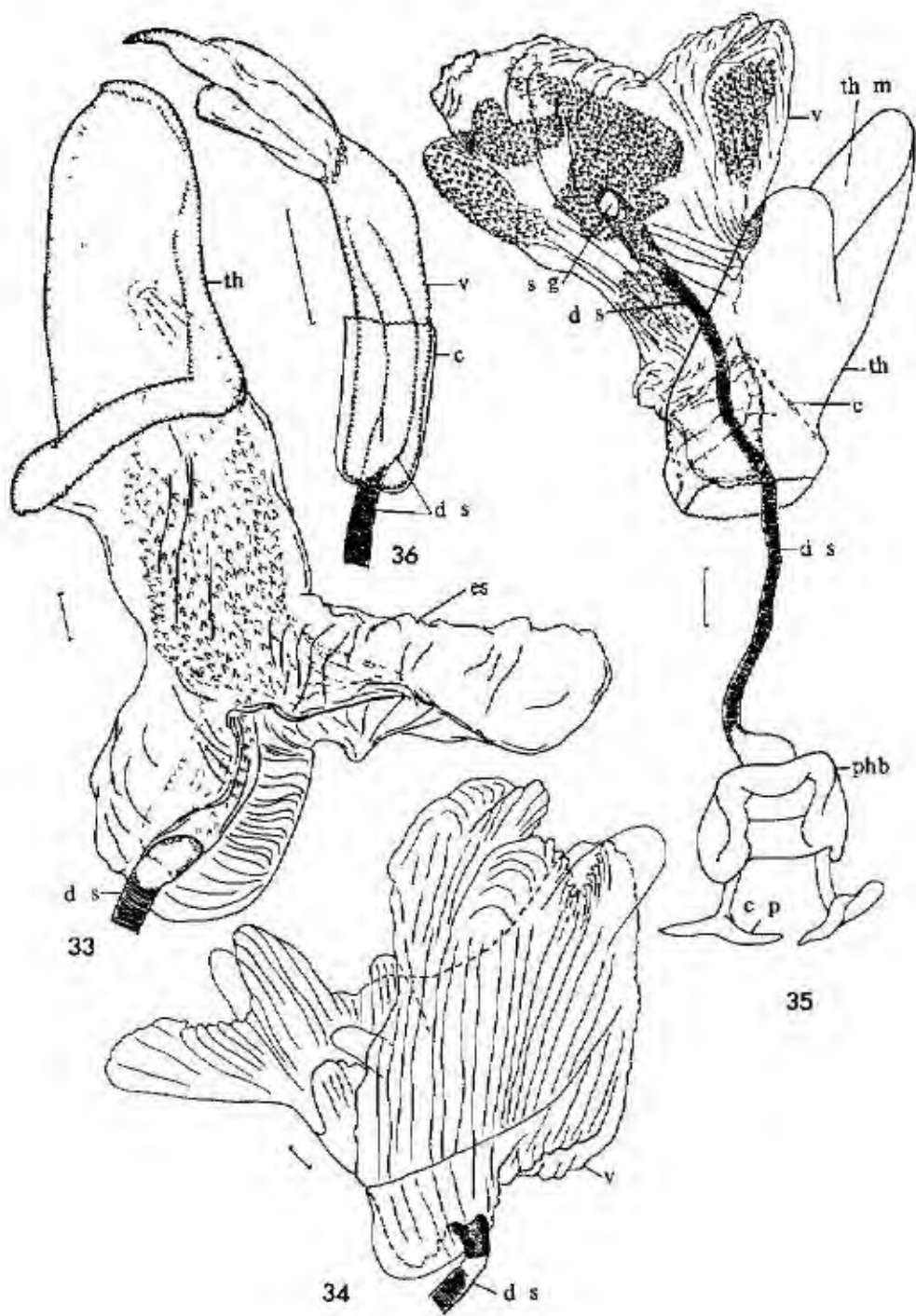
Functioning and evolution of aedeagus

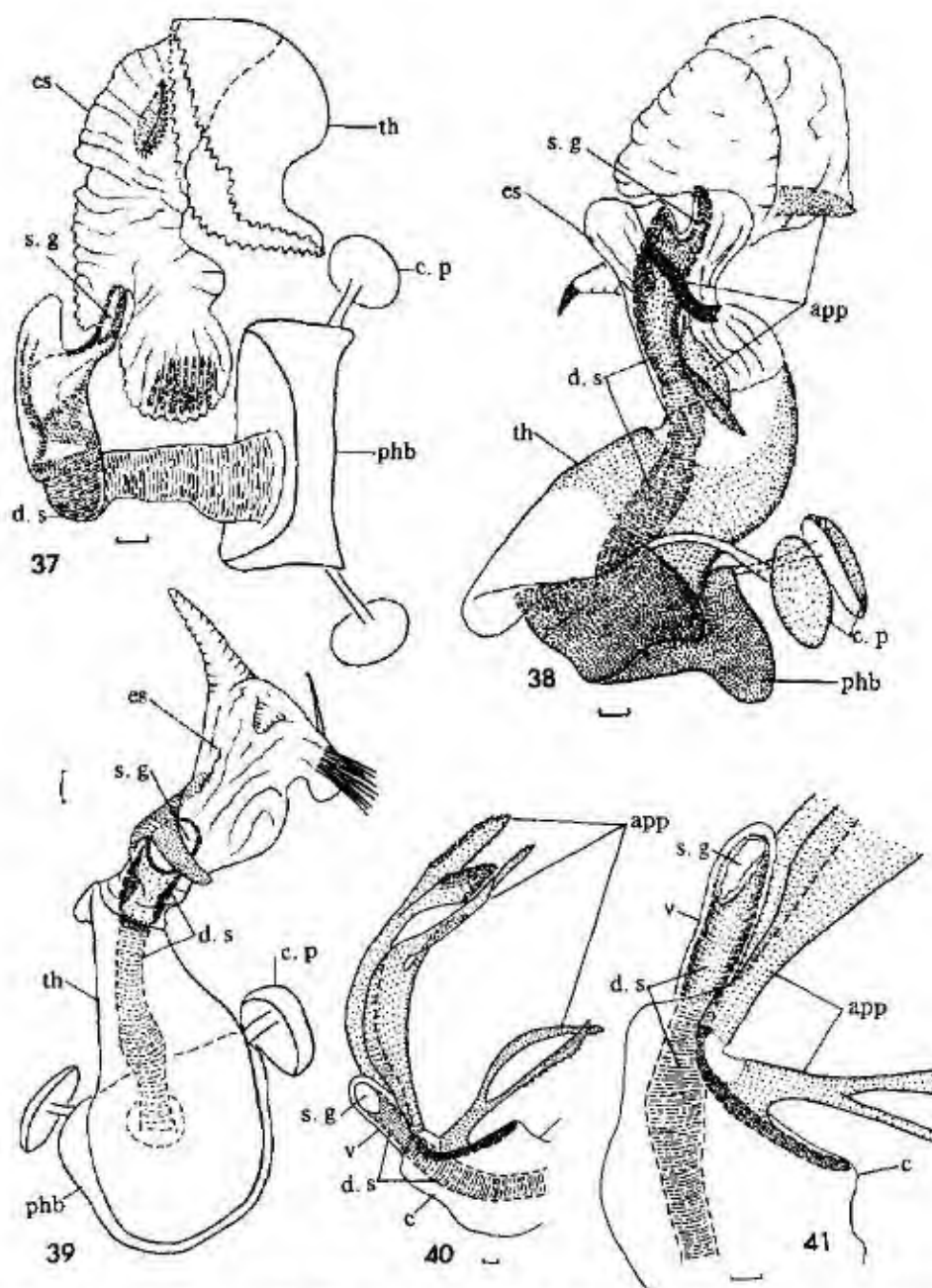
It is obvious that absence of vesica is a plesiomorphic character in the family, as it is shared by all Heteroptera, except Pentatomomorpha and Leptopodomorpha. The functioning of the aedeagus in most mirids not having a vesica is more or less similar (Fig. 2). At the beginning of copulation, by contraction of protractor muscles and probably also under pressure of body liquids, the aedeagus is shifted distally and the apex of theca is placed near the vulva of the female or inserted into the vulva. Through thin channels in the intersegmental membrane outside of the primary gonopore, the body liquids percolate in the aedeagus, under their pressure, the endosoma is everted from the theca, as a finger of a glove, and inserted into the bursa copulatrix of the female. The internal sclerotized structures, when present, become external, contacting the walls of the bursa copulatrix, anchoring the aedeagus and stimulating the female. The long elastic ductus seminis is strongly lengthened and the secondary gonopore, through which the sperma is ejaculated, occupies a mostly apical or subapical position in the inflated aedeagus. After copulation, the aedeagus is shifted by retractor muscles into a more proximal position, the pressure of body liquids decreases, and the tension of the elastic ductus seminis draws the endosoma in the theca. The process of «packing» the ductus seminis and endosoma into the theca is not well understood, apparently the parameres are of some help in this process. It is a long and complex procedure, especially in species with richly sclerotized armament of the endosoma.

Sclerotization of the distal portion of ductus seminis is apparently the first step towards formation of the vesica in Eccritotarsini and Orthotylini.

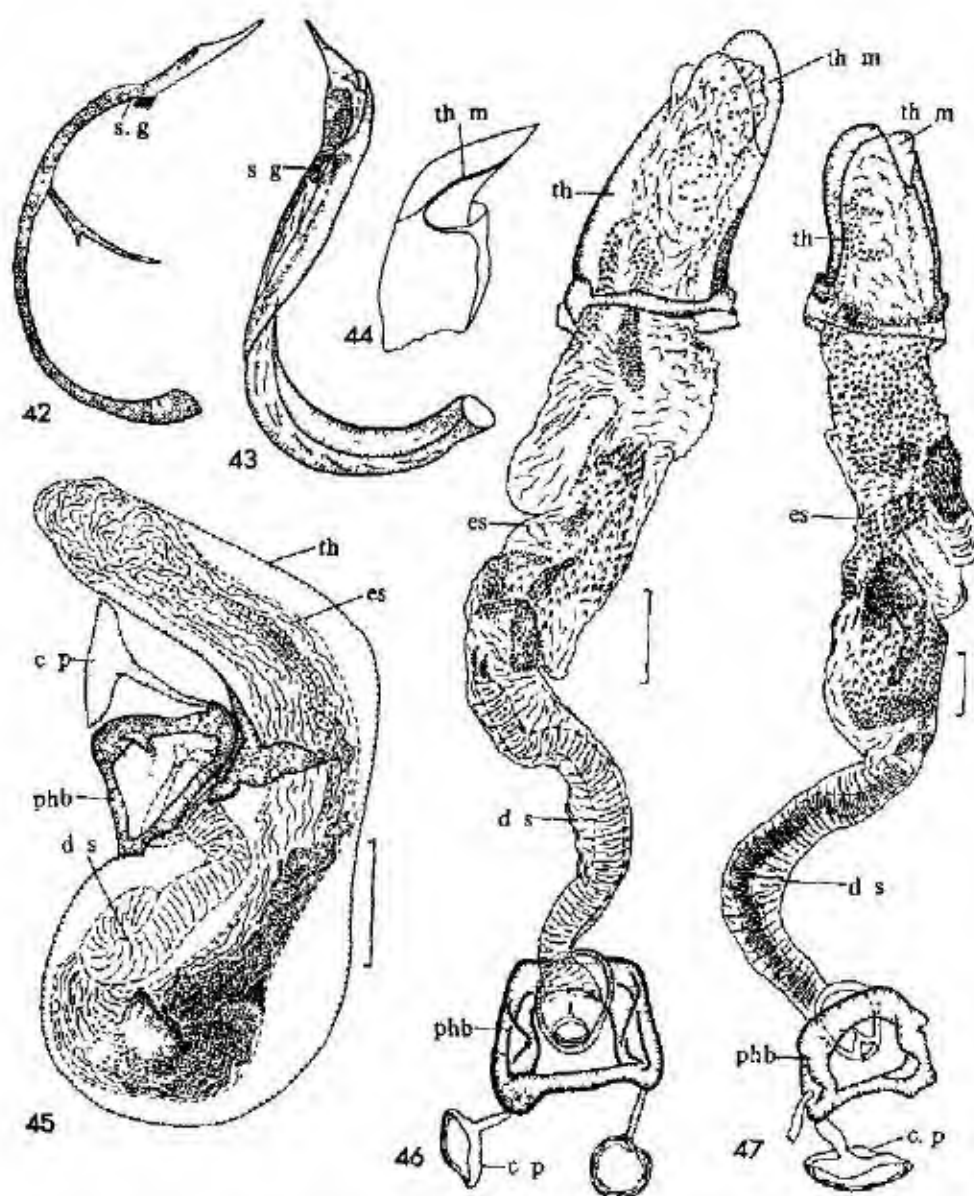
In Bryocorini, the long sclerotized portion of ductus seminis reaches the apex of theca in repose, and endosoma lacks sclerotized structures, but no vesica is formed. The firm distal portion of ductus seminis greatly simplifies its evagination and invagination during copulation (Fig. 17), but does not provide anchoring and specific stimulation in the bursa copulatrix of the female. According to observations by Kullenberg (1947), copulation in Bryocorini can be easily interrupted and its duration is short. The insertion of the aedeagus is simplified in the Bryocorini by the shifting of the opening of the male genital segment to a caudal and even partly ventral position and by the copulatory position (ventral sides of male and female abdomen are placed nearly opposite to each other).

Figs 33-36 Aedeagi of Dicyphini. 33 - *Cyrtopeltis geniculata* Fieber, aedeagus with theca separated from phallobase. 34 - *C. rufobrunnea* Lee et Kerzhner, inflated vesica. 35 - *Nesidiocoris tenuis* Reuter, erected aedeagus with theca separated from phallobase. 36 - *Macrolophus rubi* Woodroffe, vesica.





Figs 37-41. Aedeagi of Halticini (37-39) and Orthotylini (40-41). 37 - *Strongylocoris leucocephalus* Linnaeus, aedeagus with most of theca removed; 38 - *Myrmecophyes nigripes* Reuter, erected aedeagus, lateral view; 39 - *Anapus burmeisteri* Fallén, erected aedeagus, ventral view; 40-41 - *Orthotylus marginalis* Reuter (40 - apex of erected aedeagus, lateral view; 41 - area adjacent to vesica in erected aedeagus).



Figs 42-47 Aedeagi of Ptilophorini (42), Phyllini (43-44) and Termatophylini (45-47). 42, *Ptilophorus pseudoperplexus* Josifov, vesica (after Kerzhner 1988), 43-44 - *Psallus stuckelbergi* Kerzhner (after Kerzhner 1988) (43 - vesica, 44 - sclerotized apical part of theca), 45-46 - *Argyrotaenia elegans* Reuter et Poppius (45 - aedeagus in repose, lateral view, 46 - aedeagus with distal part of theca separated from phallobase and its proximal part removed), 47 - *Termatophyllum insignis* Reuter, aedeagus with distal part of theca separated from phallobase and its proximal part removed

The aedeagus of some Ecritotarsini may be considered as a further development of the structure observed in the Bryocorini: the membranous proximal part of the endosoma surrounds the long sclerotized distal portion of the ductus seminis and fuses with it, either partly (in which case an inflatable membranous lobe is formed) or completely (*Cyrtocapsus*), forming a firm and non-eversible vesica functioning in a way more or less similar to that of Phylini.

In Halticini, the small distal portion of the ductus seminis is sclerotized, but the endosoma is provided with various types of armament and retains its functions. In the expanded aedeagus, the secondary gonopore usually occupies a ventral position and is far surpassed by an everted sac of the membranous endosoma. The saddle-like apex of the sclerotized ductus seminis and various projections proximad of the secondary gonopore found in some representatives (*Labops*, *Strongylocoris*) are apparently adaptations to prevent pressing of the secondary gonopore to the wall of the bursa copulatrix and closing off the opening of the ductus seminis. The coupling of Halticini during the copulation is firm, as exemplified by relatively regular presence of copulating pairs in dry collections.

The aedeagus of Orthotylini may originate from that of Halticini with which it shares the ventral position of secondary gonopore in the everted aedeagus, but in Orthotylini the distal portion of ductus seminis is enveloped by the membranous proximal portion of endosoma forming a very simple vesica devoid of inflatable lobes or sclerotized armament. When the conjunctiva is everted during copulation, some of its branching sclerotized processes occupy a perpendicular position and anchor the aedeagus in the bursa copulatrix.

It may be suspected that the aedeagus of Phylinae originates from the type found in the Orthotylini as a result of sclerotization of the vesica, reduction of sclerotized structures on the conjunctiva, membranization of the most part of the theca and immovable connection of its strongly sclerotized apical part with the wall of the male genital segment. During the copulation (Fig. 3), the phallobase is shifted caudad, the membranous proximal part of the theca is rumpled and the vesica is nearly entirely extended through the immovable distal part of the theca. From the point of view of functioning, the aedeagus of Phylinae is the most perfect, as the pulling out and in of a firm intromittent organ is simpler than eversion and inversion of a membranous one.

Anchoring of the Phylinae aedeagus in the bursa copulatrix of the female is carried out already by the C- or S-form vesica. In some genera, especially in the Halodapini, the form of vesica is even more complex, with numerous bends. Many Pilophorini have about in the middle of vesica a process, sometimes branched; the base of this process is formed by a thin membrane; during the copulation, under pressure of liquids inside of the vesica, the membranous base becomes more firm and the process occupies a position more or less perpendicular to the main part of the vesica, thus promoting the anchoring (Fig. 5). Many Phylini (e.g., *Plagiognathus* Fieber, 1858) have 2 or 3 curved apical processes connected by membranous stripes and occupying parallel position in repose; during copulation under pressure of liquids within the vesica the apical processes are turned and form a true anchor with 2 or 3 branches (Fig. 6).

The aedeagus of the Mirinae type is characterized by a vesica with membranous lobes. During copulation (Fig. 4), under pressure of body liquids within the aedeagus, the conjunctiva is partly everted (but usually not wholly exposed), the vesica is expanded from the theca, and under pressure of liquids percolating through small openings inside the vesica its membranous lobes become inflated. With the decrease of liquid pressure after copulation, the lobes become flattened and the vesica is drawn inside the theca. Of the four groups having a vesica of the Mirinae type, Deracoricorinae (except Teratophylini) and Mirinae are undoubtedly related, but Fulvini and Dicyphini are not. It is clear that aedeagus of Mirinae type (Ecritotarsini can be also referred to this type) originated in the Miridae independently several times.

DISCUSSION

In the main, the structure of the aedeagus agrees with the subfamily and tribal classification of Miridae accepted currently. However, there are several groups the rank and position of which deserve further study. We refrain here from taxonomic changes, because they should be based on examination of many characters and more representative material.

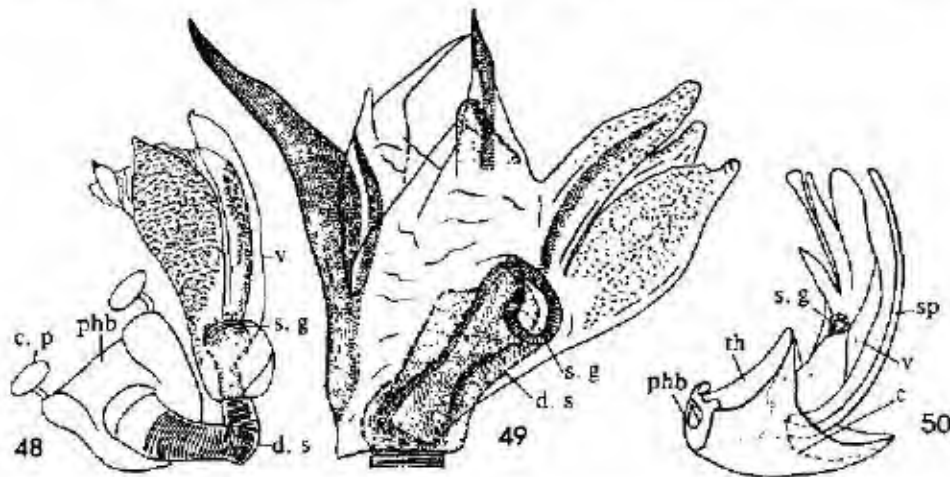
Fulviini Uhler, 1886. Subfamily status was suggested by Schmitz & Štys (1973). Their conclusion is supported by the fact that Fulviini, unlike Cylapini, have an advanced type of aedeagus with a vesica of Mirinae type.

Ecritotarsini Berg, 1883. By the structure of aedeagus, this tribe can be subdivided at least in two groups. As many genera remain not examined, it is difficult to say whether this variability is evidence for polyphyly of the tribe or not.

Dicyphini Reuter, 1883. Schuh (1976, 1995) included Monaloniini and Odoniellini in Dicyphini as subtribes. However, Dicyphini, unlike two other tribes, have an advanced type of aedeagus.

Teratophylini Reuter, 1884. This small group was originally described as a subfamily of Anthocoridae with which it shares the pterect head, then for some time considered as a separate family, and finally transferred to Miridae as a subfamily (China & Myers 1929) and placed as a tribe in Deraeocorinae (Carvalho 1952). Nevertheless, some authors (e.g. Wagner 1974a: 29, footnote, Linnavuori 1975) quite recently have accepted family or subfamily rank for this group. The placement in Deraeocorinae was mostly based on similar structure of pretarsus (hair-like parempodia and presence of a tooth at base of claws) and presence of pronotal collar. However, these characters are not decisive because they occur in various groups of Miridae. In terms of the structure of the aedeagus, Teratophylini differ from all other Deraeocorinae, and they are much more primitive.

Halticini A. Costa, 1853. Singh-Pruthi (1925) and Kelton (1959) considered that Halticini have a vesica. Wagner (1974b) accepted for them subfamily rank stating that Halticinae have a vesica of Mirinae, not of Orthotylinae type. He was followed in giving Halticini a subfamily rank by some other European authors, including the first author of this paper. Actually, Halticini, in contrast to



Figs 48–50. Aedeagi of Deraeocorini (48) and Mirini (49). 48 – *Deraeocoris serenus* Douglas et Scott, aedeagus with removed theca, 49 – *Apolygus subpulchellus* Kerzhner, inflated vesica (after Kerzhner 1988). 50 – *Capsus ater* Linnaeus, erected aedeagus (after Singh-Pruthi 1925)

Orthotylini, have no vesica, though the structure of their aedeagus may be considered as an initial step for the formation of an aedeagus of Orthotylini type. Another peculiarity of Halticini is the absence of K-structures characteristic for the female genitalia of Orthotylini (Slater 1950). The above facts show that relationships between the two tribes and the rank of Halticini deserve further study.

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BOOK REVIEW

MARGULIS L. & SCHWARZ K. V. *Five Kingdoms. An illustrated Guide to the Phyla of life on Earth. Third Edition*. New York: W. H. Freeman and Co., 1997. XX + 520 pages. Format 230×232 mm. Soft cover. Price Lstg 25.95. ISBN 0-7167-3027-8.

First author is Distinguished University Professor at the University of Massachusetts (Amherst) – she is the author and co-author of numerous monographs: *Handbook of Protozoists* (1990), *Origins of Sex* (1991), *Illustrated Glossary of Protozoists* (1992), *Symbiosis in Cell Evolution* (1993), *The Illustrated Five Kingdoms* (1994). Second author teaches in the biology department at the University of Massachusetts (Boston), she is a professional photographer of natural history. Earlier editions (1982, 1988) have been praised as “rarest of intellectual treasures – a terse visual index to the living library – a sampler of life”. In addition, translations into Spanish, Japanese and German appeared in print. As emphasized in the foreword by S. J. Gould (Museum of Comparative Zoology, Harvard University), some investigators dismiss taxonomies and their revisions as mere exercises in abstract ordering. Still, classifications express most fundamental concepts about the objects of our universe, and also record degree and amount of life’s diversity and complexity. In the preface, the authors characterize their book as an illustrated guide to the diversity of life on Earth and a comprehensive reference to both microbes and macroscopic organisms – what they look like, where they dwell, how they are related to one another, and how scientists group them. NASA scientists stressed the need of an illustrated guide to the diversity of life on Earth to inform their search for possible extraterrestrial life forms. As further emphasized, concepts of kingdoms and phyla originate in the classification proposals of scientists of the twentieth century: R. Whittaker and H. Copeland – built on earlier attempts of Linnaeus, Jussieu, Cuvier, and Haeckel to order the biota. The molecular data have most profoundly affected the view of bacteria and protozoists. The authors anticipate further classification shifts.

The volume is composed of 5 chapters which provide insights into actual knowledge of particular kingdoms. **Chapter 1** concentrates on the kingdom **Bacteria** (Prokaryotae, Procaryotae, Monera) which comprises 14 phyla divided in two subkingdoms – **Archaea** (Archaeobacteria) and **Eubacteria**. Next chapters are joined in the frame of the superkingdom **Eukarya**. **Chapter 2** presents the kingdom **Protozoists** which comprises 30 phyla of eukaryotic organisms and their immediate descendants: all algae, flagellated water molds, the slime molds and slime nets, the traditional protozoa, and some other aquatic organisms. All protozoist cells have nuclei and other eukaryotic features. Many photosynthesize (have plastids), most are aerobes (have mitochondria) and most have undulipodia (= flagella) with their kinetosome bases at some stage of their life cycle. The name of protozoists is derived from the Greek *protos* = very first and *zōstha* = creature. In this system there are no one-celled animals, traditional protozoans are placed in the Protozoists kingdom. **Chapter 3** is devoted to the kingdom **Animalia**. Animals conclude 37 phyla beginning with trichoplax (Placozoa) and poriferans (sponges) and concluding with cephalochordates and cranians. **Chapter 4** provides insights into the kingdom **Fungi** (= Mycota or Eufungi). As defined here, this kingdom is limited to eukaryotes that form resistant spores and chitinous cell walls and that are immobile at all stages of their life cycle. Featured are three phyla: Zygomycota, Basidiomycota and Ascomycota. Concluding **Chapter 5** is concerned with members of the plant kingdom **Plantae** as multicellular organisms which have a sexual stage in their life cycle. Photosynthesis by plants requires enzymes within membrane-bounded plastids. Plants include 12 phyla. Finally, there is an appendix containing a list of phyla and a tabular overview of genera mentioned in this book. For some genera common (vernacular) English names are given. Still, for most genera no common names are available. Moreover, there is a glossary of biological and ecological terms relating to certain kingdoms or phyla. The introduction to each chapter defines the general features of the entire kingdom, and it is followed by essays, each describing one phylum of that kingdom. At the top of the right-hand page of each phylum essay is a scene with one or more arrows pointing to typical habitats of the members of the phylum: temperate seashore, temperate forests, lakes and rivers, deserts and high mountains, tropical forest, tropical seas, tectonically active anoxic environment and the ocean. Each phylum is characterized by micro- or macrophotographs and corresponding line-drawings of a distinctive species or of an anatomical detail, schematic drawings of life cycles, dendrograms, cross sections, cutaway views or diagrams. In addition, there are summary-type tables, classification schemes, and more. Each chapter is concluded with a list of references.

This extraordinary volume provides a most comprehensive catalogue or picture book of the world’s living diversity of nature’s life five great kingdoms using modern taxonomical schemes. It allows readers to sample full range of life forms inhabiting our planet and familiarize themselves with new ideas on molecular systematics.

Jindřich Jira

The genus *Chilocoris* (Heteroptera: Cydnidae) in Australia

Jerzy A. Lis

Department of Zoology, University of Opole, Oleska 22, PL-45-052 Opole, Poland
e-mail: cydnus@uni.opole.pl

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Abstract. A review of Australian representatives of the genus *Chilocoris* Mayr, 1865 is presented. Following new species are described: *Ch. bicolor* sp. n. (Queensland, Northern Territory), *Ch. centrastephonides* sp. n. (Queensland, New South Wales), *Ch. entzioides* sp. n. (Queensland), *Ch. flavus* sp. n. (Northern Territory), *Ch. monticola* sp. n. (Queensland), and *Ch. obscurus* sp. n. (Queensland). A key to all Australian species of the genus is provided.

Taxonomy, review, key, new species, Heteroptera, Cydnidae, *Chilocoris*, Australia

INTRODUCTION

The genus *Chilocoris* Mayr, 1865 (of the tribe Cydnini) is the most speciose genus among the whole Cydnidae, represented by more than 70 species distributed in all major faunal regions of the Old World (Lis unpubl.).

The genus was not recorded from Australia for a long time, and only recently (Lis 1995) four its species was found to occur there (*Ch. australis* in Western Australia, *Ch. tasmanicus* in Tasmania, *Ch. barbarae* in Northern Territory, and *Ch. biroi* in Queensland).

The present paper provides a review of all (known and new) species of the genus found in Australia, among them four already recorded there, one (*Ch. neozelandicus*) recorded for the first time from Australia, and six new to the science.

A key to all the Australian genera of the tribe Cydnini (to which the genus belongs) was presented recently (Lis 1997).

MATERIAL

The paper is based on the material borrowed from the following institutions and private collections (acronyms given in the parentheses): the Natural History Museum, London, England [= former British Museum (Natural History)] (BMNH), Department of Primary Industries, Mareeba, Australia (DPI/M), J. E. Eger collection, Tampa, Florida, USA (JECT), Northern Territory Museums and Art Galleries, Darwin, Australia (NTMD), South Australian Museum, Adelaide, Australia (SAMA), Queensland Museum, Brisbane, Australia (QMB), University of Queensland Insect Collection, Brisbane, Australia (UQIC), Western Australian Museum, Perth, Australia (WAMP), Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZIPR), the author's collection at University of Opole, Department of Zoology, Opole, Poland (UODZ).

A REVIEW OF SPECIES

Chilocoris Mayr, 1865

Chilocoris Mayr, 1865: 907. Type species by monotypy: *Chilocoris nitidus* Mayr, 1865.

DIAGNOSTIC CHARACTERS. Head margins with pegs and hair-like setae. Lateral margins of pronotum not serrated. Scutellum broader than long, triangular. Evaporative area on mesopleuron large, subquadrate, covering most of the segment and reaching its lateral and posterior margins; the polished part of peritreme long, reaching or surpassing the lateral margin of metapleural evaporative area and there forming a posteriorly curved rounded lobe.

Chilocoris australis Lis, 1995

Chilocoris australis Lis, 1995: 226.

MATERIAL EXAMINED. **Western Australia:** Holotype female, Yallingup, Nr. Cape Naturaliste, S. W. Australia, Sep. 14 – Oct. 31, 1913, R. E. Turner, 1914–27; *Chilocoris australis* Lis, Holotype det. J. A. Lis (BMNH).

COMPARATIVE NOTES. *Ch. australis* is best characterised by a set of following characters: body concolorous, its length about 3.4 mm; head with 9 submarginal setigerous punctures (bearing 6 pegs and 3 hair-like setae) on each paraclypeus; ocular index about 3.6; pronotum with a transverse, interrupted medially row of punctures behind calli; a distance between anterolateral and anterior hair-like setae on pronotum shorter than a distance between the anterolateral and the medial submarginal hair-like setae; mesocorium with numerous well separated punctures almost of the same size as those on pronotum.

DISTRIBUTION. It is the only Australian species known from the Western Australia.

Chilocoris barbarae Lis, 1991

Chilocoris barbarae Lis, 1991: 301; 1995: 229.

MATERIAL EXAMINED. **Northern Territory:** 1 male, N. T. Warlock Ponds, 35 mi N. of Larrimah, 21 June 1972, at light, B. K. Head (SAMA); 1 female, N. T., 5 km E Mataranka, at light, 27 Sept. 1977, G. F. Gross, J. A. Forrest (SAMA); 1 female, N. T., Lake Woods, 15 km SW Elliot, at light, 5 Oct. 1977, G. F. Gross (SAMA); 1 female, N. T., Lake Bennett area, c. 25 km SE of Manton Dam, 29–30 Dec 1979, M. B. Malipatil, at M. V. light (NTMD); 1 female, Channel Point, N.T., via Stapleton Stn., 25 June 1982, C. Wilson, ex light trap (NMT). **Queensland:** 1 female, Cairns, QLD, 30 Sept. 1978, R. Easton (WAMP); 1 female 2 males, Crystal Cascades, Via Cairns, N. Qld., 22 Dec. 1964, H. A. Rose (UQIC); 1 female 2 males, Upper Mulgrave River, N. Qld., 1–3 Dec. 1965, G. Monteith (UQIC); 1 male, Iron Range, Cape York Pen., N. Qld., 16–23 Nov. 1965, G. Monteith (UQIC); 2 females, "The Boulders" via Babinda, N. Qld., 15 Nov. 1969, B. Cantrell (UQIC); 1 male, Somerset Dam, Qld., 19 Apr. 1965, T. Wier (UQIC); 1 male, F. W. Lake, 10 mi. N of Rocky R., Via Coen, N. Qld., 17 Dec. 1964, G. Monteith (UQIC); 1 male, NE Qld, Boulder Ck via Tully, 150 m, 24 Oct. 1983, Monteith, Yeates & Thompson, MV light in RF, clearing (QMBA); 1 female, NEQ, 17 14'S×145.25'E, 3 km W of Bones Knob, 10 Dec. 1995 – 9 Feb. 1996, Monteith, Cook, Thompson, RF pitfall traps, 1140 m (QMBA). **New South Wales:** 1 female, Walgett, N. S. W., 30 Dec. 1971, B. Cantrell (UQIC).

COMPARATIVE NOTES. *Ch. barbarae* belongs to the group of concolorous species with pronotum bearing distinct transverse impressed line behind calli. Within this group it is best diagnosed by its small body (length not exceeding 3.0 mm) and its dorsal surface covered with numerous well visible short hairs.

DISTRIBUTION. The species was described from Sulawesi (Lis 1991). It is known also from Malay Peninsula, Sumatra, Java, Madura, Peleng, Papua New Guinea, and Australia, where it previously was recorded only from the Northern Territory (Lis 1994, 1995).

Chilocoris bicolor sp. n.

(Figs 1, 3)

TYPE MATERIAL. *Holotype*: male [QUEENSLAND]: SEQ; 25 27'S×150 02'E, Taroom District, Boggomoss No. 8, 10 Sep – 11 Nov 1996, OF, P. Lawless, pitfall, 102; QMT 31379 (QMBA). *Paratypes* [QUEENSLAND]: 1 female, SEQ; 25 27'S×150 02'E, Taroom District, Boggomoss No. 8, 10 Sep – 11 Nov 1996, OF, P. Lawless, pitfall, 102 (QMBA); 1 male 1 female, SEQ; 25 27'S×150 02'E, Taroom District, Boggomoss No. 8, 11 Nov 1996 – Jan 1997, OF, P. Lawless, pitfall, 103 (QMBA, UODZ); 2 females, Heron I., SQ, 10–14 Nov. 1957, T.E. Woodward (UQIC); [NORTHERN TERRITORY]: 2 males 3 females, N. T., Katherine Low Level Native Park, 12 April 1982, R. Hanley (NTMD, UODZ); 1 female, N. T., Kakadu NP, Nourlangie Camp, 17–18 Nov 1979, M. V. light, M. B. Malipatil (NTMD); 2 females, 13 29'S 132 28'E, Gimbat Stn., N. T., 7–8 Oct. 1986, P. Horner, M. V. light (NTMD, UODZ); 1 male, N. T., Limestone Gorge, 16 02'S 130 23'E, 23–26 June 1986, M. Malipatil, Operation Raleigh 1986, in litter, Ficus (NTMD); 1 female, Northern Territory, West Alligator Mouth, 22 July 1979, WAI, G. B. Monleith, Q. M. Berlesgate No. 113, 12 12'S 132 13'E, rainforest, Sieved litter (QMBA), 1 male 1 female, Horn Islet, Pellew Group, N. T., 15–21 Feb. 1968, B. Cantrell (UQIC).

DIAGNOSIS. Among the Australian species of the genus, this one can easily be recognised by its bicolorous body (Fig. 1), with almost entire corium colourless or milky white. *Ch. bicolor* sp. n. is closely related to *Ch. biroi* in general habitus, but only a middle part of corium (mesocorium) is colourless in the latter. Additionally, both species differ in the number of pronotal submarginal hair-like setae (4–5 in *Ch. bicolor* sp. n., 3 in *Ch. biroi*).

DESCRIPTION. Body bicolorous; head, pronotum and scutellum brown, dark brown or blackish brown, corium milky white or almost colourless and translucent.

Head dorsal surface coarsely wrinkled and striated; clypeus almost parallel-sided, as long as paraclypei, and subapically with a pair of pegs; each paraclypeus with a submarginal row of 9 setigerous punctures (6 stout pegs and 3 hair-like setae); eyes red or reddish brown, ocular index 2.07–2.32; ocelli red or reddish brown, ocellar index 2.9–4.0, interocellar distance about 7–11 times longer than a distance between ocellus and the eye; antennae brown or dark brown; rostrum from pale yellowish brown to pale brown, surpassing the anterior coxae, and not surpassing the middle of mesosternum.

Pronotum trapezoid in outline, its posterolateral parts (including umbones) and sometimes also posterior margin yellowish brown or whitish yellow; pronotal disc with punctures of two types – tiny and almost indistinct distributed over entire surface, and large well visible punctures present in the posterior half of a disc and also in its anterolateral parts, and punctures forming postmedian (usually interrupted) row; umbones swollen; lateral margins with 4–5 setigerous punctures bearing long hair-like setae.

Scutellum distinctly punctured with punctures larger than those on pronotum; basal and lateral rows of punctures coarse, dense and well developed, the lateral rows not reaching the scutellar apex; scutellar disc impunctate in the basal fourth and in the extreme apex.

Corium with dark brown punctures and patch near membrane, and brown costal margins and suture between meso- and exocorium; clavus, exocorium and basal part of mesocorium sometimes whitish yellow; all punctures brown or dark brown; clavus with two rows of punctures (short, long); mesocorium with two rows of punctures paralleling clavo-corial suture, punctures in the inner row connected by dark incised line, the remaining surface of mesocorium sparsely, almost evenly punctured with smaller, sometimes indistinct punctures; exocorium impunctate except for two rows of punctures parallel to mesocorium; membrane semihyaline, sometimes slightly embrowned, extending well beyond the posterior extremity of abdomen.

Propleuron alutaceous, brown or blackish brown, its postero-lateral parts yellowish brown; median depression with a few darker punctures close to coxae; meso- and metapleuron with evaporatoria typical of the genus.



Fig. 1. *Chilocoris bicolor* sp. n.: general habitus.

Legs from yellowish brown to brown, not specifically modified; tibial spines dark reddish brown. Abdominal sternites from brown to blackish brown, medially impunctate, laterally with numerous setigerous puncture bearing shining long adjacent hairs; posterior margins of segments accompanied by a row of shining hairs. Paramere as in Fig. 3.

Measurements (in mm) (male followed by female): body length 3.44–4.36, 3.20–4.12; body width 1.89–2.43, 1.67–2.29; head length 0.62–0.71, 0.55–0.64; head width 0.85–1.14, 0.79–0.96; pronotum length 1.07–1.44, 0.93–1.31; pronotum width 1.87–2.42, 1.59–2.17; scutellum length 0.89–1.15, 0.78–1.07; scutellum width 1.14–1.61, 0.93–1.41; antennal segments: 0.17–0.21 : 0.07–0.13 : 0.28–0.33 : 0.26–0.31 : 0.35–0.37, 0.15–0.19 : 0.05–0.10 : 0.22–0.31 : 0.23–0.28 : 0.30–0.36.

DISTRIBUTION. Known from the Northern Territory and SE Queensland. Distributed most probably also in the northern parts of Queensland, but till now not found there.

ETYMOLOGY. The name of the species is connected with its sharply bicolourous body.

Chilocoris biroi Horváth, 1919

Chilocoris biroi Horváth, 1919: 257.

Chilocoris biroi Lis 1995: 229

MATERIAL EXAMINED. **Queensland** 1 male 4 females, Tully Falls, N. Qld., 770 m, 8 Dec 1989 – 5 Jan 1990, Monteith, Thompson & Janetzki, pitfall & intercept traps (QMBA); 1 male 4 female, Davies Creek Road, 20 km ESE Mareeba, N. Qld., 4–13 Dec 1988, 750 m, Monteith & Thompson, flight intercept trap (QMBA); 1 male 1 female, NEQ, 15 25'S×145 07'E, Endeavour R. (Covacevich), 5 Nov – 9 Dec 1995, Monteith, Cook & Roberts, flight intercept, 20 m (QMBA); 2 females, SEQ, 27 03'S 152 41'E, Mt Mee, 320m, 29 Nov 1991 – 8 Jan 1992, D. J. Cook, RF intercept (QMBA); 2 males 1 female, NEQ, 17 12'S×145 40'E, Danbulla Scient. Res., 10 Dec – 7 Feb 1996, Monteith & Cook, intercept trap, 740 m (QMBA); 3 males 2 females, SEQ, 28 11'S×153 11'E, Lower Coomera, 3 Dec 94 – 9 Jan 1995, G. Monteith & H. Janetzki, intercept trap, 350 m (QMBA); 3 males 6 females, NEQ, 18 39'S×145 52'E, Wallman Falls Rd, Junction, 650 m, 5–12 Feb 1996, Monteith, flight intercept, RF (QMBA); 4 males 5 females, NE Qld., 15 47'S 145 14'E, Shiptons Flat, 280 m, 6 Dec 1990 – 19 Jan 1991, Qld. Mus. & ANZSES, flight intercept trap (QMBA); 4 males 6 females, NE Qld., 15 43'S 145 17'E, Big Tableland, 618 m, 21 Dec 1990 – 9 Jan 1991, ANZSES Expedition, flight intercept trap (QMBA); 6 males 11 females, NEQ, 17 28'S 146 01'E, Polly Creek (Hasenpusch), 25 Nov 1994 – 10 Jan 1995, Monteith & Hasenpusch, Flt intercept trap, 50 m (QMBA); 1 male 3 females, NE Qld., 2.7 km W of Cape Tribulation (Site 5A), 5–9 Jan 1981, 400 m, G. B. Monteith, RF, baited pitfall traps (QMBA); 2 males 2 females, NE Qld., 1.5 km NW of Cape Tribulation (Site 1), 23 Sept – 7 Oct 1982, 10 m, Monteith, Yeates & Thompson, baited pitfall traps, RF (QMBA); 6 males 3 females, NE Qld., 2.5 km W of Cape Tribulation (Site 5), 20–23 Apr 1983, 180 m, G. B. Monteith & D. K. Yeates, RF, baited pitfall traps (QMBA); 2 males 5 females, Mossman Bluff Track, 4–10 km W Mossman, N Qld., 20 Dec 1989 – 15 Jan 1990, Monteith, Thompson & ANZSES, Site 4, 600 m, flt. intercept (QMBA); 1 male 3 females, Karnak Devil's Thumb, 8–12 km NW Mossman, NQ, 26 Dec 1989 – 15 Jan 1990, ANZSES Expedition, Site 4, 300 m, flt. intercept (QMBA); 1 male 2 females, West Claudie R., Iron Range, N. Qld., 3–10 Dec 1985, G. Monteith & D. Cook, flight trap, rainforest (QMBA); 2 males 4 females, 27 30'S 152 58'E, Indooroopilly, Qld., 17–21 Dec 1990, A. Kerejshuk (ZIPR); 4 females, Bluewater Range, 50 km WNW Townsville, NEQld., 6–9 Dec 1986, 700 m, Monteith, Thompson & Hamlet, flight intercept trap (QMBA); NE Qld., 19 16'S 147 03'E, Mt Cleveland summit, 23 Mar – 13 May 1991, D. Cook, rainforest, pitfall & intercept traps (QMBA); 1 male 1 female, Lake Placid nr Cairns, NQ., 18 Dec 1974, M. B. Malipatil, leaf litter (UQIC); 1 male 1 female, Lockerbie Scrub via Bamaga, Qld., Apr 7–14, 1977, R. I. Storey (DPIM); 1 female, NEQ, 17 26'S 145 42'E, Hughes Road, Topaz, 6 Dec 1993 – 25 Feb 1994, Monteith Cook & Janetzki, RF pitfalls, 650 m (QMBA); 1 female, Mt Coot-tha, Brisbane, Qld., 13–20 March 1971, G. B. Monteith, ex leaf litter (UQIC); 1 male, Qld., 20 20'S×148 45'E, Mt Hayward, 350 m, 19–20 Nov 1992, Monteith Thompson Cook & Janetzki (QMBA); 1 male, NEQ, 17 24'S 145 41'E, Westcott Rd., Topaz, 6 Dec 1993 – 25 Feb 1994, Monteith Cook & Janetzki, RF intercept, 680 m (QMBA); 1 male, Tolga Scrub, N. Qld., 750 m, 9 Dec 1989 – 14 Jan 1990, Monteith Thompson & Janetzki, pitfall & intercept traps (QMBA); 1 male, Kentworth State Forest, SE Qld., 5 Dec 1966, G. Monteith (UQIC); 1 male, 40 Mile Scrub via Mt Garnet, N. Qld., 20–25 May 1984, Storey & Walford-Huggins, intercept trap, Site No. 13 (DPIM).

COMPARATIVE NOTES. *Ch. biroi* was redescribed in detail by Lis (1993). For comparative characters see remarks to the previous species.

DISTRIBUTION. The species was described from New Guinea (Horváth 1919). Recently found also in Queensland (Lis 1995).

Chilocoris centrostephoides sp. n.

(Figs 2, 4)

TYPE MATERIAL. **Holotype**, male: [QUEENSLAND]: NEQ, 17.26°S×145.42°E, Hughes Road, Topaz, 6 Dec 1993 – 25 Feb 1994, Monteith Cook Janetzki, RF intercept, 650 m; QMT 46171 (QMBA). **Paratypes**: [QUEENSLAND]: 3 males 7 females, NEQ, 17.26°S×145.42°E, Hughes Road, Topaz, 6 Dec 1993 – 25 Feb 1994, Monteith Cook Janetzki, RF intercept, 650 m (QMBA, UODZ); 2 males 1 female, NEQ, 17.26°S×145.42°E, Hughes Road, Topaz, 650 m, Sept – Dec 1993, Monteith & Breeden, pitfall trap (QMBA, UODZ); 4 females, NEQ, 17.26°S×145.42°E, Hughes Road, Topaz, 650 m, July – Sept 1993, Monteith & Breeden, flight intercept traps (QMBA, UODZ); 1 male, Sluice Ck., 9 km WSW Millaa Millaa, NEQ, 5–14 Dec 1988, 1150 m, Monteith & Thompson, flight intercept trap (QMBA); 1 female, Aust., Qld., NE, Mt Fisher, 7 km SW Millaa Millaa, Kjellberg Rd., 3 May 1983, G. Monteith, QM Berlesate No. 578, 17.33°S 145.33°E, rainforest, 1000 m, Sieved litter (QMBA); Qld., 21.34°S×149.12°E, Upper E. Funnel Ck., 16 Nov 1992, 450 m, Monteith Thompson & Janetzki, Perythrum (QMBA); 2 males 2 females, Paluma Dam Rd., N. Qld., Site 4, 750 m, Nov 17 – Dec 8 1990, Monteith & Seymour, flight intercept trap (QMBA, UODZ); 2 males 7 females, Paluma Dam Rd., N. Qld., Site 1, 900 m, 8 Dec 1990 – 5 Feb 1991, Monteith & Seymour, flight intercept trap (QMBA, UODZ); 1 male 2 females, Paluma Dam Rd., N. Qld., Site 3, 800 m, 8 Dec 1990 – 5 Feb 1991, Monteith & Seymour, flight intercept trap (QMBA); 2 females, Paluma Dam Rd., N. Qld., Site 3, 800 m, Nov 17 – Dec 8 1990, Monteith & Seymour, pitfall trap (QMBA); 1 male 2 females, N. E. Qld., 15.43°S 145.17°E, Big Tableland N. E. Cnr, 20 Dec 1990 – 8 Jan 1991, ANZSES Expedition, flight intercept, 800 m (QMBA); 1 female, N. E. Qld., 15.43°S 145.17°E, Big Tableland, 618 m, 21 Dec 1990 – 9 Jan 1991, ANZSES Expedition, flight intercept (QMBA); 2 males, NEQ, 15.57°S×145.08°E, Mt Boolbun Sth summit, 5 Nov 1995 – 11 Jan 1996, Monteith Cook & Roberts, intercept trap, 950 m (QMBA, UODZ); 1 male, Aust., Qld., NE, Hann Tbl., N. End, 14 Dec 1995, Cook Monteith & Thompson, QM Berlesate 903, 16.49°S×145.11°E, rainforest, 100 m, leaf litter (QMBA); 2 females, NEQ, 17.23°S×145.46°E, Bartle Frere, W. Base, 7 Mar – 15 May 1995, Monteith & Hasenpusch, pitfall traps, 700 m (QMBA, UODZ); 1 female, Davies Ck Road, 20 km ESE Mareeba, N. Qld., 4–13 Dec 1988, 750 m, Monteith & Thompson, flight intercept trap (QMBA); 1 male, NEQ, 16.04°S×145.28°E, Pilgrim Sands, 5 m, 19 Nov – 10 Dec 1993, Monteith Roberts & Cook, flight intercept trap (QMBA); 1 female, NE Qld., Emerald Ck, Lamb Range, 11 Oct 1982, Monteith Yates & Thompson, pyrethrum knockdown, RF (QMBA); 1 female, NE Qld., Emerald Ck, Lamb Range, 11 Oct 1982, Monteith Yates & Thompson, QM Berlesate No. 468, 17.06°S 145.37°E, rainforest, 950 m, sieved litter (QMBA); 1 male 1 female, Mt Tyson, 2 km W Tully, NE Qld., 7 May 1983, D. K. Yates, QM Berlesate No. 588, 17.55°S 145.54°E, rainforest, sieved litter (QMBA); 3 males 3 females, NEQ, 17.24°S 145.41°E, PEI Road, Topaz, 6 Dec 1993 – 25 Feb 1994, Monteith Cook & Janetzki, RF intercept, 580 m (QMBA); 1 male, Aust., Qld., NE, Boonjie, 13 km ESE Malanda, 8 Dec 1988, G. Monteith G. Thompson, QM Berlesate No. 814, 145.45°E 17.25°S, rainforest, 700 m, sieved litter (QMBA); 1 female, NEQ, 16.56°S 145.51°E, Mt Murray Prior, 770 m, 31 Oct – 8 Dec 1995, Monteith & Cook, pitfall traps (QMBA); 1 female, SEQ, 25.27°S×150.02°E, Taroom District, Boggomoss No. 8, 11 Nov 1996 – Jan 1997, OF, P. Lawless, pitfall, 103 (QMBA); 1 female, Davies Ck Road, 20 km ESE Mareeba, 26 Nov 1985, D. Yates D. Cook, QM Berlesate No. 686, 17.02°S 145.35°E, rainforest, 900 m, sieved litter (QMBA); 1 male, Aust., Qld., Lamb Ra., 19 km SE Mareeba, 11 Dec 1988, G. Monteith G. Thompson, QM Berlesate No. 822, 145.34°E 17.06°S, rainforest, 1200 m, Moss (QMBA); 1 female, NE Qld., 22 km SE of Mareeba, 900 m, 4 Nov 1983, D. K. Yates & G. I. Thompson, pyrethrum knockdown in RF (QMBA); 1 male, Tully Falls, N. Qld., 750 m, 8 Dec 1989 – 5 Jan 1990, Monteith Thompson & Janetzki, pitfall & intercept traps (QMBA); 3 females, Charmillin Ck Xing, 950 m, Tully Falls Rd., N. Qld., 8 Dec 1989 – 5 Jan 1990, Monteith Thompson & Janetzki, pitfall & intercept traps (QMBA); 4 males 6 females, NEQ, 17.28°S 146.01°E, Polly Creek, Hasenpusch, 25 Nov 1994 – 10 Jan 1995, Monteith & Hasenpusch, flight intercept trap, 50 m (QMBA, UODZ); 1 male 1 female, NEQ, 17.28°S 146.01°E, Polly Creek, Hasenpusch, 7 Mar – 15 May 1995, Monteith & Hasenpusch, intercept trap, 100m (QMBA, UODZ); 1 female, NE Q., 16.54°S 145.42°E, Whitfield Range, 550 m, 28 Aug – 19 Oct 1991, Monteith & Janetzki, pitfall & intercept traps (QMBA); 1 female, Mt Lewis Rd., N. E. Qld., 22 km from Highway, 18 Dec 1989 – 13 Jan 1990, Monteith Thompson & ANZSES, Site 3, 1000 m, flight intercept (QMBA); 2 males 2 females, Aust., Qld., NE, Mt Finnigan, 37 km S Cooktown, 21 Apr 1982, Monteith Yates Cook, QM Berlesate No. 410, 15.49°S 145.17°E,

rainforest, 1050 m, sieved litter (QMBA, UODZ); 1 female, Mt Finnigan, 850–1100 m, 37 km S Cooktown, N. Qld., 19–22 Apr 1982, Monteith Yeates Cook, pyrethrum knockdowns (QMBA); 1 male, Baldy Mtn road, SW of Atherton, N. Qld., 1000 m, 10 Oct 1980, G. B. Monteith, rainforest (QMBA); 2 females, NEQ, 17.23°S 145.46°E, Bartle Frere, W. Base, 25 Nov 1994 – 10 Jan 1995, Monteith & Hasenpusch, Flt. intercept trap, 50 m (QMBA); 2 females, 2 km SE Mt Spurgeon via Mt Carbine, N. Qld., 20 Dec 1988 – 4 Jan 1989, Monteith Thompson & ANZSES, 1100 m, RF Flt. intercept (QMBA); 1 female, 3 km SE Mt Spurgeon via Mt Carbine, N. Qld., 21 Dec 1988 – 4 Jan 1989, Monteith Thompson & ANZSES, 1100 m, RF Flt. intercept (QMBA); 1 male 1 female, NE Qld., 3.0 km W of Cape Tribulation (Site 6), 20 Sept – 7 Oct 1982, 500 m, Monteith Yeates & Thompson, baited pitfall traps, RF (QMBA, UGDZ); 3 males 3 females, NE Qld., 1.5 km NW of Cape Tribulation (Site 1), 23 Sept – 7 Oct 1982, 0 m, Monteith, Yeates & Thompson, rainforest pitfall traps (QMBA); 1 female, 3.0 km W of Cape Tribulation (Site 6), 2 Oct 1982, 500 m, Monteith, Yeates & Thompson, OM Berlesate No.



Fig. 2. *Chilocoris centrostephoides* sp. n.: general habitus.

439, 16°04'S 145°27'E, rainforest, 500 m, sieved litter (QMBA); 1 female, NE Qld, Oliver Ck., 7 km S of Cape Tribulation, 5–9 Jan 1983, 10 m, G. B. Monteith, RF baited pitfall traps (QMBA, UODZ); 2 males 2 females, Tully R. Xing, 10 km S Koombuloomba Dam, N Qld., 8 Dec 1989 – 4 Jan 1990, 750 m, Monteith Thompson & Janetzki, pitfall & intercept traps (QMBA); 1 female, NTQ, 1.5 km N Tully R. Xing, S Koombuloomba Dam, 8 Dec 1989 – 4 Jan 1990, 750 m, Monteith Thompson & Janetzki, pitfalls & intercepts (QMBA); 1 male 1 female, Lake Escham, N Qld., 750 m, 9 Dec 1989 – 14 Jan 1990, Monteith Thompson & Janetzki, pitfall & intercept traps (QMBA); 1 female, Lambs Head, 10 km W Edmonton, N Qld., 1200 m, 10 Dec 1989 – 8 Jan 1990, Monteith Thompson & Janetzki, rainforest pitfalls (QMBA); 2 females, Kirrama Range, N E. Qld., Douglas Ck Rd., 800 m, 10 Dec 1986 – 11 Jan 1987, Monteith Thompson & Hamlet, RF, flight intercept trap (QMBA); 1 female, Karnak – Devil's Thumb, 8–12 km NW Mossman, NQ, 26 Dec 1989 – 15 Jan 1990, ANZSES Expedition, Site 10, 1080 m, flt. intercept (QMBA); 2 males 4 females, Mossman Bluff Track, 5–10 km W Mossman, N Qld., 17–31 Dec 1988, Monteith Thompson & ANZSES, Site 8 1180 m, Site 9 1260 m, Site 10 1300 m, flt. intercept (QMBA, UODZ); 9 males 11 females, Mossman Bluff Track, 5–10 km W Mossman, N Qld., 20 Dec 1989 – 15 Jan 1990, Monteith Thompson & ANZSES, Site 1 250m, Site 4 600 m, Site 5 760 m, Site 6 860 m, Site 7 1000 m, Site 8 1180 m, flt. intercept (QMBA, UODZ); 2 males 2 females, Mossman Bluff Track, 5–10 km W Mossman, N Qld., 16–30 Dec 1988, Monteith Thompson & ANZSES, Site 4 600 m, Site 6 860 m, flt. intercept (QMBA); 3 males 4 females, North Summit, Bakers Blue Mt., 17 km W Mt Molloy, N Q., 1–18 Jan 1990, 1000 m, ANZSES, flt. intercept, Site 2 (QMBA, UODZ); 1 male 1 female, NE Qld., 2.5 km N Mt Lewis via Jaitlen, 3 Nov 1983, D. Yeates & G. Thompson, QM Berlesate No. 610, 16°34'S 145°16'E, rainforest, 1040 m, sieved litter (QMBA); 1 male 1 female, Bellenden Ker Range, NQ, Cableway Base Stn., 100 m, 17 Oct – 9 Nov 1981, Earthwatch/Qld. Museum, Baited window trap (QMBA); 1 male 4 females, NEQ, 17.24°S 145.41°E, Westcott Rd., Topaz, 6 Dec 1993 – 25 Feb 1994, Monteith Cook & Janetzki, RF intercept, 680 m (QMBA, UODZ); 1 female, Upper Mulgrave River, N Qld., 1–3 Dec 1965, G. Monteith (UQIC); 1 male, Cairns dist., trapped by sticky seeds of *Pisonia brunnemana*, F. P. Dodd (SAMA). [NEW SOUTH WALES]: 1 female, 30.22°S 152.44°E Austr., NSW, Dorrigo Nat. Park, Dorrigo Camp, 13–15 Nov. 1990, A. Kirejtshuk (ZIPR).

DIAGNOSIS. The species is the only one in the genus with distinct denticle on either lateral margin of pronotum (Fig. 2). At first sight, it is somewhat similar in the general shape of pronotum to representatives of the genus *Centrostephus* Horváth, 1919, for instance *C. parumpunctatus* (Signoret, 1884). For other diagnostic characters see the key to species.

DESCRIPTION. Body polished, slightly alutaceous, concolorous (Fig. 2), from yellowish brown through brown to dark castaneous.

Head dorsally wrinkled, punctured with a U-shaped row of punctures between eyes, and with a patch of smaller punctures between ocelli; clypeus as long as or slightly longer than paraclypei, subapically with a pair of pegs, medially broadened and somewhat elevated; each paraclypeus with a submarginal row of 9 setigerous punctures (6 pegs and 3 hair-like setae); eyes brown or reddish brown, sometimes silver with reddish or brownish tinge, ocular index 2.40–3.21; ocelli from brown to reddish brown, ocellar index 3.0–4.0, interocellar distance about 2–5 times longer than a distance between ocellus and the eye; antennae slightly paler in shade than the head; rostrum from yellowish brown to brown, reaching middle coxae.

Pronotum subrectangular, its disc with a transverse, usually interrupted medially row of large punctures behind callal areas; anterior lobe impunctate except for setigerous punctures and a patch of small punctures behind the head and a few punctures laterally; the posterior lobe with numerous small punctures and over a dozen irregularly scattered large punctures; lateral margins distinctly carinated and slightly broadened in anterior three fourths, bearing 3 submarginal long hair-like setae, the base of posterior submarginal hair-like setae with small denticle; ventral short hairs well visible; umbones swollen.

Scutellum with basal and lateral rows of punctures well developed, the lateral rows not reaching the scutellar apex, the basal with less punctures than the lateral; disc medially with several large, usually darker punctures.

Corium punctured with punctures smaller than those on the scutellar disc; clavus with two rows of punctures (short, long); mesocorium with two rows of punctures paralleling clavo-corial suture,

punctures in the inner row usually connected by an incised line, the remaining surface with numerous punctures close to membrane and scutellum; exocorium impunctate except for a row of punctures parallel to mesocorium; costa without setigerous punctures; membrane semihyaline, pale brown or brown, extending well beyond the posterior extremity of abdomen.

Propleuron polished, but sometimes slightly alutaceous, almost totally impunctate except for a few punctures close to coxae; meso- and metapleuron with evaporatoria not specifically modified.

Legs pale brown or yellowish brown, not specifically modified; tibial spines brown.

Abdominal sternites polished, almost totally impunctate except for segmental sutures accompanied by sparse rows of punctures; posterior parts of segments with a few long hairs, the lateral parts with single hairs. Paramere as in Fig. 4.

Measurements (in mm) (male followed by female): body length 2.15–3.18, 2.29–3.29; body width 1.14–1.64, 1.19–1.64; head length 0.39–0.46, 0.41–0.47; head width 0.51–0.66, 0.51–0.65; pronotum length 0.61–0.95, 0.59–0.92; pronotum width 1.12–1.63, 1.16–1.61; scutellum length 0.58–0.85, 0.61–0.86; scutellum width 0.69–1.01, 0.69–1.00; antennal segments: 0.14–0.17 : 0.04–0.07 : 0.23–0.33 : 0.23–0.32 : 0.35–0.49, 0.13–0.18 : 0.04–0.06 : 0.25–0.32 : 0.24–0.31 : 0.36–0.44.

DISTRIBUTION. Known from Queensland and New South Wales.

ETYMOLOGY. The name is connected with the external similarity of the new species to representatives of the genus *Centrostephus*.

Chilocoris entzioides sp. n.

(Figs 5, 6)

TYPE MATERIAL. **Holotype**: male: {QUEENSLAND}: Aust., Qld., NE, West Claudie R, Iron Range, 8 Dec 1985, G. Monteith, QM Berlesate No. 697, 12 45'S 143.14'E, rainforest, 50 m, sieved litter; QMT 46172 (QMBA).

DIAGNOSIS. Among the Australian species with a transverse row of punctures on the pronotal disc, this one can easily be recognised by the presence of 6 submarginal setigerous punctures (3 pegs and 3 hair-like setae) on each paraclypeus (in contrary to 9 submarginal setigerous punctures found in all other species of the group). In this character the new species is related to *Ch. entzii* Horváth, 1919 (New Guinea, Bismarck Archipelago), but differs distinctly from the latter in the shape of parameres.

DESCRIPTION. Body concolorous, castaneous, highly polished, with puncturation as in Fig. 6.

Head slightly wrinkled, dorsally impunctate except for setigerous punctures; clypeus apically somewhat narrowing, as long as paraclypei, and with a pair of sharply ended pegs; each paraclypeus with a submarginal row of 6 setigerous punctures (3 pegs getting shorter towards the eye, and 3 hair-like setae); eyes whitish silver with reddish tint, ocular index 1.86; ocelli reddish brown, ocellar index 2.9, interocellar distance about 7 times longer than a distance between ocellus and the eye; antennae yellowish brown; rostrum pale yellowish brown, surpassing middle coxae.

Pronotum weakly punctured; anterior part of its disc impunctate except for a few punctures laterally, the posterior part sparsely punctured and bearing distinct (interrupted medially) row of dark punctures behind callal areas; all punctures with short, not well visible whitish hair-like bristles; umbones only slightly swollen; lateral margins with 3 submarginal setigerous punctures bearing long hair-like setae.

Scutellum distinctly punctured with a few punctures blackish brown larger than those on pronotum; basal and lateral rows of punctures well developed, the lateral rows not reaching the scutellar apex; margins of scutellum (except in the apex) blackish brown.

Corium punctured with almost colourless punctures distinctly smaller than those on scutellum; clavus with two short rows of punctures; mesocorium with two rows of punctures paralleling clavo-

corial suture and several smaller irregularly scattered punctures bearing short hair-like bristles; exocorium impunctate except for two rows of punctures close to mesocorium; costa without setigerous punctures; membrane semihyaline, whitish, slightly surpassing the tip of abdomen.

Propleuron alutaceous; median depression with a few punctures close to coxae; meso- and metapleuron with evaporatoria typical for the genus.

Legs yellowish brown, not specifically modified; tibial spines reddish brown, tarsi whitish yellow.

Abdominal sternites castaneous, slightly alutaceous, impunctate except for a row of punctures close to anterior margin of each segment; the posterior and lateral parts of segments with shining hairs. Paramere as in Fig. 5.

Measurements (in mm): body length 2.95; body width 1.68; head length 0.51; head width 0.75; pronotum length 0.95; pronotum width 1.63; scutellum length 0.83; scutellum width 0.98; antennal segments: 0.15 : 0.07 : 0.29 : 0.33 : 0.46.

DISTRIBUTION. Known only from the northern part of Queensland (Cape York Peninsula).

ETYMOLOGY. The name reflects close affinities of the new species to *Ch. entzii*.

Chilocoris flavus sp. n.

(Fig. 7)

TYPE MATERIAL. Holotype: female; [NORTHERN TERRITORY]: N. T., 12.40'S 132.30'E, 5th Alligator Inn, 7-9 July 1979, G. Monteith & D. Cook, Qld. Mus. No. 94; QMT 46173 (QMBA).

DIAGNOSIS. The species is best diagnosed by a set of following characters: body ovate and concolorous, pronotal disc with distinct transverse row of punctures behind calli, each paraclypeus with a submarginal row of 9 setigerous punctures (6 pegs and 3 hair-like setae). *Ch. flavus* sp. n. is similar to *Ch. tasmanicus* and *Ch. australis* in a general habitus, but it is distinctly smaller (2.3 mm in length; the two other species 3.4-4.5 mm).

DESCRIPTION. Body concolorous, pale brown, with puncturation as in Fig. 7.

Head dorsally slightly striated and with a few large punctures in front of the ocelli; clypeus almost parallel-sided, as long as paraclypei, and subapically with a pair of dark brown sharply ended pegs; each paraclypeus with a submarginal row of 9 setigerous punctures (6 pegs and 3 hair-like setae); eyes reddish brown, ocular index 2.6; ocelli reddish brown, ocellar index 2.7, interocellar distance about 6 times larger than a distance between ocellus and the eye; antennae slightly paler than a head; rostrum yellowish brown, surpassing anterior coxae.

Pronotum weakly punctured; its anterior half almost impunctate, single punctures present behind head and in the postero-lateral parts; the posterior half with distinct (interrupted medially) row of large dark brown punctures, and about a dozen dark punctures behind the latter; umbones swollen; lateral margins with 3-4 setigerous punctures bearing long hair-like setae.

Scutellum punctured with punctures somewhat larger than those on pronotum; basal and lateral rows of punctures dense and well developed, the lateral ones not reaching the scutellar apex; disc impunctate in the basal fourth, the remaining surface with several punctures.

Corium weakly punctured with punctures smaller than those on pronotum and scutellum; clavus with one irregular row of dark brown punctures; mesocorium translucent, almost impunctate except for two rows of dark brown punctures paralleling clavo-corial suture and several irregularly scattered punctures in the posterior part; exocorium almost impunctate except for a row of punctures paralleling a suture between meso- and exocorium; membrane colourless and translucent, large, surpassing the tip of abdomen.

Propleuron yellowish brown, slightly alutaceous; median depression with a few punctures close to coxae; meso- and metapleuron with evaporatoria typical of the genus.

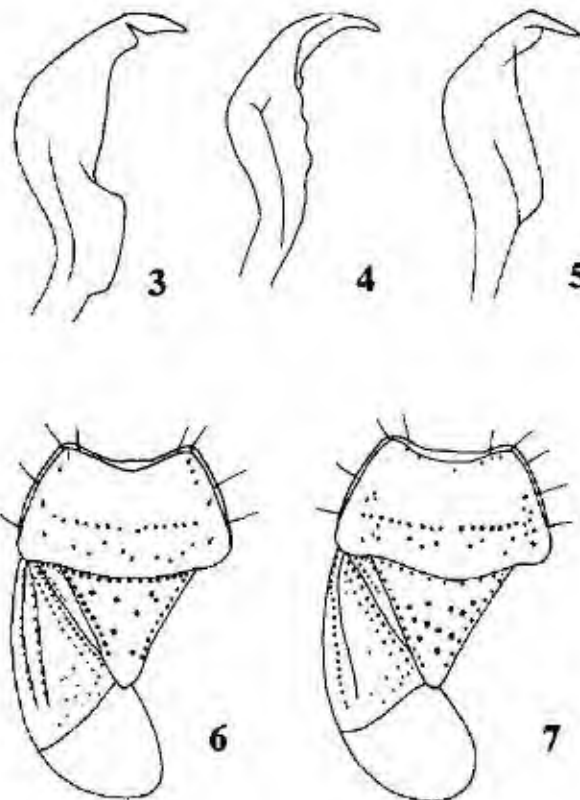
Legs whitish yellow, not specifically modified; tibial spines dark brown.

Abdominal sternites yellowish brown, impunctate and polished, in lateral parts with well visible short light hair-like bristles; posterior margins of segments accompanied by longer light hairs.

Measurements (in mm): body length 2.31; body width 1.30; head length 0.29; head width 0.53; pronotum length 0.66; pronotum width 1.19; scutellum length 0.58; scutellum width 0.74; antennal segments: 0.11 : 0.05 : 0.19 : 0.17 : 0.24.

DISTRIBUTION. Known only from the Northern Territory.

ETYMOLOGY. The name is given to show the body colour of the holotype specimen of the new species.



Figs 3-7. 3-5 - paramere, 6-7 body puncturation: 3 - *Chilocoris bicolor* sp. n., 4 - *Chilocoris ventroscephoides* sp. n., 5-6 - *Chilocoris entzaoides* sp. n., 7 - *Chilocoris flavus* sp. n.

***Chilocoris monteithi* sp. n.**
(Figs 8, 9)

TYPE MATERIAL. **Holotype** male [QUEENSLAND] NEQ, 17 28'S 146 01'E, Polly Creek, Hasenpusch, 25 Nov 1994 – 10 Jan 1995, Monteith & Hasenpusch, Flt intercept trap, 50 m, QMT 46174 (QMBA). **Paratypes** [QUEENSLAND] 4 males 7 females, NEQ, 17 28'S 146 01'E, Polly Creek, Hasenpusch, 25 Nov 1994 – 10 Jan 1995, Monteith & Hasenpusch, Flt intercept trap, 50 m (QMBA, UODZ), 1 male 3 female, NEQ, 17 26'S 145 42'E, Hughes Road, Topaz, 6 Dec 1993 – 25 Feb 1994, RF intercept, 650 m (QMBA), 6 females, Davies Ck Road, 20 km ESE Maroocha, N Qld, 4–13 Dec 1988, 750 m, Monteith & Thompson, flight intercept trap (QMBA, UODZ), 1 male 1 female, NEQ, 17 28'S 146 01'E, Stone Ck, Hasenpusch, 1 Oct – 1 Nov 1995, J Hasenpusch, intercept trap 100 m (QMBA), 3 males, C Qld, 21 52'S 147 18'E, Upper Hall Ck, via Camilla, 4 Dec 96 – 5 Apr 1997, G Monteith & B Mulder, intercept, RF at creek (QMBA, UODZ), 3 males 2 females, NE Q 16 54'S 145 42'E, Whitfield Range, 550 m, 28 Aug – 19 Oct 1991, Monteith & Janetzki, pitfall & intercept traps (QMBA, UODZ), 1 male, Russel R at Bellenden, Ker Landing, N Q, 5 m, Nov 1–9 1981, Earthwatch/Qld Mus, QM Berlesate No 349, 17 16'S 145 57'E, Palm-swamp, sieved litter (UODZ), 1 male, Russel R at Bellenden, Ker Landing, N Q, 5 m, 24 Oct – 9 Nov 1981, Earthwatch/Qld Mus, Baited window trap (QMBA), 1 male 2 females, Tully Falls, N Qld, 750 m, 8 Dec 1989 – 5 Jan 1990, Monteith, Thompson & Janetzki, pitfall & intercept traps (QMBA, UODZ), 1 male 1 female, NEQ, 16 04'S 145 28'E, Pilgrim Sands, 5 m, 19 Nov – 10 Dec 1993, Monteith Roberts & Cook, flight intercept trap (QMBA), N E Qld, 19 16'S 147 03'E, Mt Cleveland, 500 m, Jan – 12 Mar 1991, A Graham, rainforest traps (QMBA), 1 male, NE Qld, 1.5 km NW of Cape Tribulation (Site 1), 23 Sept – 7 Oct 1982, 0m, Monteith, Yeates & Thompson, baited pitfall traps, RF (QMBA), 1 male, NE Qld, 1.5 km NW of Cape Tribulation (Site 1), 23 April 1983, G B Monteith D K Yeates, QM Berlesate No 526, 16 05'S 145 28'E, rainforest, 0 m, sieved litter (QMBA), 2 males, Queensland, NE Q Bells Gap, Sarina Ra, 26 Apr 1979, G B Monteith, QM Berlesate No 67, 21 20'S 149 09'E, rainforest, sieved litter (QMBA), 1 male, Aust, Qld, NE, West Claude R, Iron Range, 8 Dec 1985, G Monteith, QM Berlesate No 697, 12 45'S 143 14'E, rainforest, 50 m, Sieved litter (QMBA), 1 male, West Claude R, Iron Range, N Qld, 3–10 Dec 1985, G Monteith & D Cook, flight trap, rainforest (QMBA), 1 male, Lake Braham, N Qld, 750 m, 9 Dec 1989 – 14 Jan 1990, Monteith Thompson & Janetzki, pitfall & intercept traps (QMBA), 1 male, NEQ, 17 24'S 145 41'E, PEI Road, Topaz, 6 Dec 1993 – 25 Feb 1994, Monteith Cook & Janetzki, RF intercept, 580 m (QMBA), 1 male, Queensland, Pandanus Ck, Cathu SF, 20 Apr 1979, G B Monteith, QM Berlesate No 45, 20 48'S 148 33'E, open forest, 80 m, sieved litter (QMBA), 1 female, NEQ, 13 25'S 145 07'E, Endeavour R (Covacevich), 5 Nov – 9 Dec 1995, Monteith, Cook & Roberts, flight intercept, 20 m (QMBA), 1 female, NEQ, 17 17'S 145 54'E, Bellenden Ker Base Sta, 28 Aug – 20 Oct 1991, 100 m, Monteith & Janetzki, flight intercept trap (QMBA), 1 female, NEQ, 17 35'S 145 35'E, Maalan SF on Hwy, 25 Nov 1994 – 10 Jan 1995, Monteith & Hasenpusch, Flt intercept trap, 850 m (QMBA), 1 female, NEQ, 17 22'S 145 42'E, Lamins Hill, 1 Dec 1993 – 25 Feb 1994, Monteith & Hasenpusch, RF pitfalls, 880 m (QMBA)

DIAGNOSIS *Ch monteithi* sp. n. is the only Australian species of the genus with pronotal disc bearing neither a transverse impressed line behind calli nor a transverse row of punctures. It is closely related to *Ch peterseni* Froeschner, 1967 (New Britain, New Guinea) in the general habitus and body punctuation, but can easily be separated from the latter by the shape of paramere, and its smaller body size (length 3.17–4.00 mm in *Ch monteithi* sp. n., 4.05–4.95 mm in *Ch peterseni*). **DESCRIPTION** Body polished, concolorous, castaneous or dark castaneous, generally weakly punctured (Fig. 8)

Head dorsally more or less alutaceous, slightly wrinkled and impunctate except for setigerous punctures, clypeus as long as paraclypei, narrowed basally, subapically with a pair of pegs, each paraclypeus with a submarginal row of 6–8 setigerous punctures (3 large and well visible pegs, 2 small and sometimes indistinct pegs, and 3 hair-like setae), eyes castaneous or reddish brown, ocular index 1.87–2.24, ocelli from brown to reddish brown, ocellar index 3.0–3.9, interocellar distance about 3.7–5.0 times longer than a distance between ocellus and the eye, antennae brown or pale brown, rostrum brown or pale brown, reaching middle coxae

Pronotum trapezoid in outline, its disc undivided into two lobes, its anterior part impunctate except for setigerous punctures and sometimes for single punctures laterally, the posterior part with over a dozen scattered darker punctures, entire disc usually with more or less visible very small

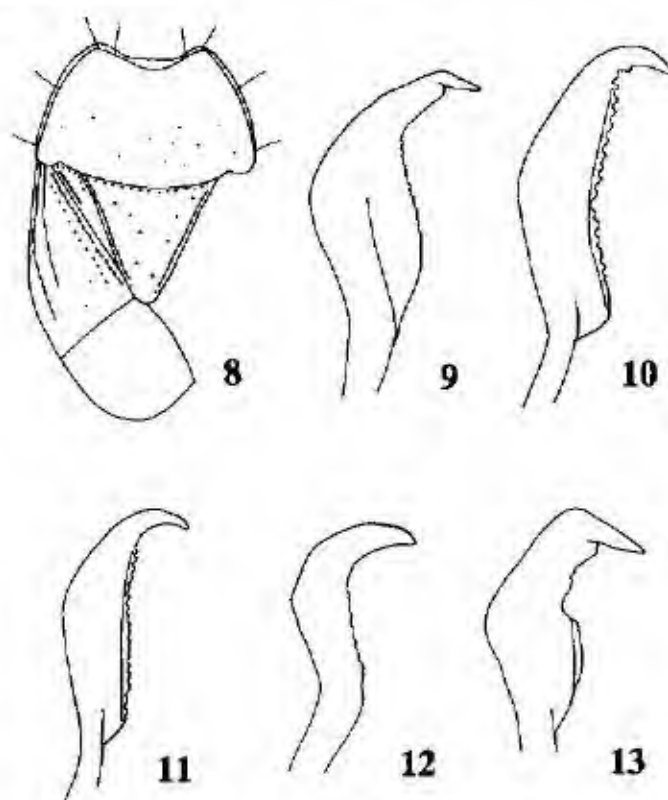
punctures; lateral margins with 3 submarginal setigerous punctures bearing long hair-like setae, ventral short hairs visible; umbones swollen.

Scutellum with basal and lateral rows of punctures well developed, the lateral rows not reaching the scutellar apex, all rows usually darker than the scutellar disc; the latter only with a few darker punctures larger than those on pronotum.

Corium weakly punctured with punctures smaller than those on scutellum; clavus with two rows (short, long) of punctures, usually darker than the remaining surface; mesocorium with two rows of punctures paralleling clavo-corial suture, punctures in the inner row connected by an incised line, the remaining surface with scattered small and usually colourless punctures close in the apical part; exocorium impunctate except for a row of punctures parallel to mesocorium; costa without setigerous punctures; membrane extending well beyond the posterior extremity of abdomen, translucent, sometimes embrowned.

Propleuron more or less alutaceous, depression usually darker than the convexities and bearing a few punctures close to coxae; meso- and metapleuron with evaporatoria not specifically modified.

Legs not specifically modified, from pale brown to dark brown, tarsi pale brown, tibial spines blackish brown or dark castaneous.



Figs 8-13. 8 - body puncturation, 9-13 - paramere: 8-9 - *Chilocoris monteuhl* sp. n., 10 - *Chilocoris obscurus* sp. n., 11 - *Chilocoris tasmanicus* Lis., 12 - *Chilocoris neozelandicus* Larivière et Froeschner, 13 - *Chilocoris biroi* Horváth

Abdominal sternites from highly polished to alutaceous, almost totally impunctate except for segmental sutures accompanied by sparse rows of punctures; posterior parts of segments with long brown hairs, the lateral parts with a few long and protruding hair-like setae and several shorter, adjacent hairs. Paramere as in Fig. 9.

Measurements (in mm) (male followed by female): body length 3.17–3.98, 3.29–4.00; body width 1.73–2.10, 1.76–2.22; head length 0.48–0.64, 0.51–0.60; head width 0.75–0.88, 0.76–0.91; pronotum length 0.90–1.25, 1.01–1.36; pronotum width 1.68–2.02, 1.72–2.15; scutellum length 0.87–1.01, 0.85–1.11; scutellum width 1.05–1.25, 1.05–1.33; antennal segments: 0.15–0.19 : 0.07–0.11 : 0.30–0.35 : 0.33–0.39 : 0.43–0.50, 0.16–0.18 : 0.07–0.10 : 0.33–0.37 : 0.35–0.40 : 0.45–0.51.

DISTRIBUTION. Known only from Queensland.

ETYMOLOGY. The new species is dedicated to Dr. G. B. Monteith, an outstanding specialist on Australian Aradidae and a curator of Heteroptera at the Queensland Museum.

Chilocoris neozealandicus Larivière et Froeschner, 1994

Chilocoris neozealandicus Larivière et Froeschner, 1994: 245.

MATERIAL EXAMINED. **Queensland**: 1 male, Qld, Mary Cairncross Pk, 6 km SE Maleny, 11 Nov. 1989, M. Purcell (JECT); 1 female, Brisbane, 21.4.57, Haseler (UQIC); 1 male 1 female, SEQ, 28.15S×153.16E, Springbrook Repeater, 9 Jan – 9 Feb 1995, G. B. Monteith, intercept traps, 1000 m (QMBA); 1 male, Kenilworth State Forest, via Kenilworth, S. E. Qld., 20 Oct. 1972, B. K. & J. A. Cantrell (UQIC). **New South Wales**: 3 males 2 females, 30.22'S 152.44'E Austr., NSW, Dorrigo Nat. Park, Dorrigo Camp, 13–15 Nov. 1990, A. Kirejtshuk (ZIPR).

COMPARATIVE NOTES. The species was described and figured in detail by Larivière & Froeschner (1994) and Larivière (1995). It represents the group of species that is characterised by pronotal disc divided into two lobes by distinct transverse impressed line behind calli. *Ch. neozealandicus* is similar to *Ch. obscurus* sp. n. in a body size and vestiture, but can easily be distinguished from the latter by its impunctate head, and the shape of parameres (Figs 10, 12).

DISTRIBUTION. Described from New Zealand and treated as an endemic species (Larivière & Froeschner 1994, Larivière 1995); previously not recorded from Australia.

Chilocoris obscurus sp. n. (Fig. 10)

TYPE MATERIAL. **Holotype** male: [QUEENSLAND]: NEQ, 16.49'S 145.40'E, Saddle Mtn, 640 m, 10 Dec 1995 – 7 Feb 1996, Monteith & Cook, pitfall traps, QMT 46175 (QMBA). **Paratypes**: [QUEENSLAND]: 1 male, NEQ, 16.49'S 145.40'E, Saddle Mtn, 640 m, 10 Dec 1995 – 7 Feb 1996, Monteith & Cook, pitfall traps (QMBA); 1 male, SEQ, 26.12'S 151.44'E, Keysland, 29 Sept – 5 Dec 1994, G. Monteith, intercept trap, open forest (QMBA); 2 males 1 female, Davies Ck Road, 20 km ESE Marceba, N. Qld., 4–13 Dec 1988, 750 m, Monteith & Thompson, flight intercept trap (QMBA, UODZ); 1 male, SEQ, 25.29'S×150.08'E, Boggom, 30, via Taroom, 14 Nov 96 – Jan 1997, Cook & Monteith, Baited flight intercept, 057 (UODZ); 1 female, Aust. Qld. SE, Taroom District, Boggomoss 8, 12 Nov 1996, G. B. Monteith, QM Bordergate No. 914, 25.27'S×150.02'E, Open forest, 180 m, Sieved litter (QMBA); 1 female, Tully R. Xing, 10km S Koombulooomba Dam, N. Qld., 8 Dec 1989 – 4 Jan 1990, 750 m, Monteith Thompson & Janetzki, pitfall & intercept traps (QMBA); 3 females, C. Qld., 21.52'S 147.18'E, Upper Hall Ck, via Camilla, 4 Dec 96 – 6 Apr 1997, G. Monteith & E. Mulder, intercept, RF at creek (QMBA, UODZ); 1 female, SEQ, 25.27'S×150.02'E, Taroom District, Boggomoss No. 8, 11 Nov 1996 – Jan 1997, QF, P. Lawless, pitfall, 103 (QMBA).

DIAGNOSIS. The new species is related to *Ch. neozealandicus* in general habitus and the type of body vestiture. For diagnostic characters see the key and notes to the previous species.

DESCRIPTION. Body concolorous, polished, slightly alutaceous, from brown to dark castaneous.

Head dorsally wrinkled, and punctured with numerous small and a few large punctures; clypeus almost parallel-sided, slightly narrowing apically, as long as paraclypei, and with a pair of stout pegs; each paraclypeus with a submarginal row of 9 setigerous punctures (6 stout pegs and 3 hair-like setae); eyes red or reddish brown, ocular index 1.70–2.27; ocelli red or reddish brown, ocellar index 2.5–4.0, interocellar distance about 6–10 times longer than a distance between ocellus and the eye; antennae from brown to dark castaneous; rostrum from pale brown to brown, surpassing middle of mesosternum.

Pronotum trapezoid, anteriorly narrowed; its disc divided into two lobes by well visible, transverse (not interrupted medially, and not reaching the lateral margins) incised line bearing several punctures; anterior lobe with numerous evenly spaced very small and almost indistinct punctures, and a few large punctures laterally; posterior lobe with numerous evenly spaced almost indistinct punctures, and with over a dozen irregularly scattered large punctures; umbones only slightly swollen; lateral margins with 3 setigerous punctures bearing long hair-like setae.

Scutellum weakly punctured on a disc, punctures larger than those on pronotum; lateral rows of punctures well visible, punctures usually connected by an incised line, and not reaching the scutellar apex; basal part with several punctures in a row.

Corium distinctly punctured with punctures only slightly smaller than those on scutellum; clavus with two rows of punctures (short, long); mesocorium with two rows of punctures paralleling clavo-corial suture; the entire remaining surface of mesocorium with evenly spaced punctures; exocorium impunctate, except for two rows of punctures close to mesocorium, and a few punctures in its apical part; membrane semihyaline, embrowned, extending well beyond the posterior extremity of abdomen.

Propleuron alutaceous, almost impunctate; median depression with a few coarse punctures close to coxae; meso- and metapleuron with evaporatoria typical of the genus.

Legs from yellowish brown to brown, not specifically modified; tibial spines castaneous or dark castaneous.

Abdominal sternites from brown to dark castaneous, alutaceous, impunctate, each sternite laterally and posteriorly with shining adjacent hairs. Paramere as in Fig. 10.

Measurements (in mm) (male followed by female): body length 3.90–5.50, 3.75–4.91; body width 2.08–2.91, 2.04–2.69; head length 0.60–0.75, 0.56–0.75; head width 0.89–1.13, 0.92–1.03; pronotum length 1.29–1.58, 1.18–1.42; pronotum width 2.05–2.61, 1.99–2.37; scutellum length 0.98–1.22, 0.99–1.20; scutellum width 1.29–1.66, 1.25–1.46; antennal segments: 0.18–0.20 : 0.08–0.10 : 0.26–0.40 : 0.27–0.39 : 0.33–0.45, 0.18–0.19 : 0.07–0.08 : 0.28–0.35 : 0.28–0.33 : 0.34–0.43.

DISTRIBUTION. Known from SE and NE Queensland.

ETYMOLOGY. The name of the new species is connected with its concolorous dark body surface.

Chilocoris tasmanicus Lis, 1995

Chilocoris tasmanicus Lis, 1995. 226.

MATERIAL EXAMINED **Tasmania**. Holotype female, Tasmanna, Hobart; Holotype, *Chilocoris tasmanicus* Lis, det. J.A. Lis (BMNH) **Queensland** 2 males 2 females, SEQ, 28.15S×153.16E, Springbrook Repeater, 9. Jan – 9. Feb 1995, G. B. Monteith, intercept traps, 1000 m (QMBA); 1 male, Aust. Qld SE, Springbrook Repeater, 14 Mar 1997, Monteith & Russell, QM Berlesate No. 922, 28.15S×153.16E, rainforest, 1000 m, sieved litter (QMBA); 1 male 2 females, SEQ, 28.02'S 152.23'E, Bare Rock, 2 km N of Mt Cordaux, 1100 m, 31 Dec 93 – 20 Feb 1994, G. Monteith, intercept (QMBA); 1 male 4 females, SEQ, 26.16'S 151.25'E, Key Property at Brigooda, Bottom site, 15 Dec 94 – 26 Jan 1995, G. B. Monteith, intercept trap, vine scrub (QMBA); 1 male 1 female, Bellenden Ker Range, NQ, Summit Tv Stn, 29 Apr – 2 May 1983, G. B. Monteith D. Cook, QM Berlesate No. 575, 17.16'S 145.51'E, rainforest, 1560 m, moss on ground (QMBA); 2 males, O'Reilleys Guesthouse, Larimington Nat. Pk., Qld., 14 Dec. 1981, G. Monteith & D. Yeates, QM Berlesate No. 377, rainforest, sieved litter

(QMBA), 1 female, Lam Nar Pk, Qld., 20 May 1962, B. Bateman (UQIC), 1 male, Lever's Plateau, Via Rathdowney, 4 April 1964, S. Qld., J. E. Dunwoody (UQIC), 1 male, SEQ, 28 12'S 153.12'E, Tullawalla, Binns Burra, 3 Dec 94 – 9 Jan 1995, G. Monteith & H. Janczki, intercept trap, 950 m (QMBA), 1 female, NEQ, 19 07'S 146 23'E, Mt Halifax summit, 1050 m, Jan – 20 Mar 1991, A. Graham, pitfalls & intercept (QMBA); 1 female, N. E. Qld., 19 16'S 147.03'E, Mt Cleveland, 560 m, Jan – 12 Mar 1991, A. Graham, rainforest traps (QMBA), 1 female, Queensland, NEQ, Eungella N. P., palm lookout, 18 Apr 1979, G. B. Monteith, QM Berlesate No 32, 21 10S 141 31E, rainforest, 700 m, stick brushings (QMBA), 2 females, Windsor Tableland, N. Qld., 27 Dec 88 – 8 Jan 1989, E. Schmidt & ANZSES, Site 6, flt. intercept (QMBA)

COMPARATIVE NOTES. *Ch. tasmanicus* is closely related to *Ch. australis* (for separating characters see the key). Since the former species was hitherto known only by the holotype female, the complementary notes to its original description are presented below:

Body from brown to dark castaneous, 3.51–4.46 mm in length, 1.95–2.44 mm in width. Eyes from dark brown to dark castaneous, ocular index 2.11–3.40, ocellar index 2.4–4.0, interocellar distance about 4.0–5.5 times a distance between ocellus and the eye. Paramere as in Fig. 11.

DISTRIBUTION. Known from Tasmania and Queensland.

Key to the Australian species of the genus *Chilocoris*

1. Pronotum divided into two lobes by distinct transverse impressed line behind calli. 2
- Pronotum without a transverse impressed line behind calli. 4
2. Body length not exceeding 3.0 mm (1.9–2.7), dorsal surface with numerous distinct short hairs. *Ch. barbarae* Lis
- Body length exceeding 3.0 mm (3.7–5.5); dorsal surface with single hairs present only on the body margins. 3
3. Head wrinkled, and distinctly punctured between eyes; paramere as in Fig. 10. *Ch. obscurus* sp. n.
- Head only wrinkled, impunctate between eyes, paramere as in Fig. 12. *Ch. neozelandicus* Larivière et Froeschner
4. Pronotal disc weakly and almost evenly punctured; a transverse row of punctures behind calli absent; paramere as in Fig. 9. *Ch. monteithi* sp. n.
- Pronotal disc with distinct, usually interrupted medially transverse row of punctures behind calli; paramere not as in Fig. 9. 5
5. Body bicolorous, corium entirely or at least mesocorium colourless and translucent. 6
- Body concolorous, mesocorium of the same colour as pronotum and scutellum, never colourless. 7
6. Corium almost entirely colourless or milky white, except apical brown patch and brown punctures (Fig. 1); paramere as in Fig. 3. *Ch. bicolor* sp. n.
- Clavus and exocorium as coloured as scutellum, mesocorium at least medially colourless or milky white, paramere as in Fig. 13. *Ch. birai* Horváth
7. Each paraclypeus with 6 submarginal setigerous punctures bearing 3 pegs and 3 hair-like setae; eyes large, ocular index about 1.9, paramere as in Fig. 5. *Ch. entzioides* sp. n.
- Each paraclypeus with 9 submarginal setigerous punctures bearing 6 pegs and 3 hair-like setae; eyes smaller, ocular index about 2.1–3.6; paramere not as in Fig. 5. 8
8. Body elongated, almost parallel-sided, 1.9–2.1 times longer than broad (Fig. 2); lateral margins of pronotum with denticle at the base of the posterior submarginal hair-like setae, paramere as in Fig. 4. *Ch. centrostephoides* sp. n.
- Body ovate, 1.7–1.9 times longer than broad; lateral margins of pronotum without denticle, paramere not as in Fig. 4. 9
9. Body small, about 2.3 mm in length. *Ch. flavus* sp. n.
- Body larger, exceeding 3.0 mm in length (3.4–4.5 mm). 10
10. Eyes larger, ocular index about 2.1–3.4; body exceeding 3.5 mm (3.5–4.5 mm) in length; paramere as in Fig. 11. *Ch. tasmanicus* Lis
- Eyes smaller, ocular index about 3.6; body not exceeding 3.5 mm (3.4 mm) in length, paramere not as in Fig. 11. *Ch. australis* Lis

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BOOK REVIEW

KLUG W S & CUMMINGS M R **Concepts of Genetics**. Fifth edition. Upper Saddle River, New Jersey: Prentice-Hall, Simon & Schuster/A Viacom Co., 1997. XXI+703 pp, appendices 58 pp. Format 210×275 mm. Hardbound, price USD 44.50. ISBN 0-13-531062-8.

First author is currently professor of biology at the College of New Jersey in Ewing. The second author is currently associate professor in the Department of Biological Sciences and in the Department of Genetics at the University of Illinois in Chicago. As indicated in the preface, this publication is now well into its second decade providing support to students as they study one of the most fascinating scientific disciplines. First edition occurred in print in 1983. This edition reflects progress over the past decade, namely in the technology of recombinant DNA, in genetics of cancer and of the immune response, and in population and evolutionary genetics.

The volume consists of 25 chapters divided into three well-balanced parts. Each chapter begins with brief chapter concepts. Introduced has been a series of 15 essays, each containing a section referred to as **Genetics, Technology, and Society**. These essays appear near the end of most chapters and are pointed up by colour. In conclusion, outlined are summaries, key terms, insights and solutions, problems and discussion questions, extra-spicy problems, and references for further readings.

At the beginning, the first chapter is concerned with the introduction to genetics while stressing the historical context and basic concepts of genetics, investigative approaches and the impact of genetics on society, including the eugenics, the misguided application of science.

Part one – Heredity and the Phenotype – incorporating chapters 2 through 9 provides insights into general terms in genetics. In the chapter on cell division and chromosomes described are cell structure, various aspects of chromosomes, mitosis and cell division, genetic regulation of the cell cycle, meiosis and sexual reproduction, the synaptonemal complex, and more. In following chapters attention is paid to Mendelian genetics and Mendelian ratios, to linkage, crossing over, and chromosome mapping, to recombination and mapping in bacteria and bacteriophages, to extensions of genetic analysis, notably to genotypic expression, continuous variations and polygenes, heritability, and to use of haploid organisms in linkage and mapping studies. In concluding chapters extranuclear inheritance, chromosome variation and sex determination are looked at.

Part two – Molecular Basis of Heredity – embracing chapters 10 through 17 concentrates attention upon ribonucleic acids and their functions in genetics. Discussed are structure and analysis of DNA as genetic material in bacteria, bacteriophages and eukaryotic organisms, RNA as genetic material, DNA replication and recombination, storage and expression of genetic information, proteins as end products of genetic expression including inborn errors of metabolism. There follows a chapter dealing with gene mutation, DNA repair, and transposable elements. Two chapters are devoted to recombinant DNA technology, while enlightening the cloning DNA in host cells, constructing DNA libraries, sequencing and PCR analysis, DNA fingerprinting, genome analysis, and more. Concluding chapter examines genomic organization of DNA viruses, bacteria and eukaryotic cells.

Part three – Advanced topics in genetic analysis – composed of chapters 18 through 25 ensures coverage of regulations of gene expression in bacteria, phages and eukaryotes. Following chapter concentrates on cancer as a genetic disorder at the cellular level that involves mutation of genes, taking the role of environmental factors and viruses into account. Final topics are dedicated to the genetic basis of immune response, to genetics of behaviour, population genetics, and to evolutionary aspects of genetics.

In addition to the text, there are three appendices: appendix A contains information on physical and chemical techniques that have been important in molecular genetics, appendix B offers an extensive glossary of terms relevant to genetics, appendix C summarizes solutions to selected problems and discussion questions. Illustrations are situated practically on each page. The majority of figures are presented in colours. Line drawings present chromosome and genetic maps, karyotypes and genotypes, biological cycles, clinical syndromes, modelled structures of biomolecules, schemes of genetic processes and procedures, diagrammatic representations, pedigrees, and more. Micro- and macrophotographs depict prokaryotic and eukaryotic cells and organisms, laboratory procedures, clinical aspects, histological sections, computer-generated colour-enhanced electron micrographs, etc. In short, it takes a delight in turning the leaves of this excellent and user-friendly textbook.

Jindřich Jira

Two new Ambrysinæ (Heteroptera: Naucoridae) from Minas Gerais, Brazil

Nico NIESER¹⁾, Afonso PELLÍ²⁾ & Alan LANE DE MELO³⁾

¹⁾Hertog Eduardstr. 16, 4001 RG Tiel, The Netherlands; e-mail: ifang.oi@net.tiel.nl

²⁾Estação de Pesquisa e Desenvolvimento Ambiental de Volta Grande, CEMIG, Caixa Postal 17,
CEP 38120-000, Conceição de Alagoas, MG, Brazil.

³⁾Departamento de Parasitologia, ICB, Universidade Federal de Minas Gerais, Caixa Postal 486-CEP30161-
970, Belo Horizonte, MG, Brazil; e-mail: aldemelo@mono.icb.ufmg.br

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Abstract. Two new species of Ambrysinæ from Minas Gerais (Brazil) are described: *Ambrysus (Melloella) lamprus* sp. n. and *Carvalhoella stysi* sp. n. The genus *Melloella* De Carlo, 1935 is reduced to subgeneric rank within *Ambrysus* Stål, 1862 and keys to species of Ambrysinæ in southern Brazil and northern Argentina are given.

Taxonomy, new species, new status, key, Heteroptera, Naucoridae, Ambrysinæ, Neotropical region

INTRODUCTION

Within the framework of preparing identification keys to the water bugs of the Brazilian state of Minas Gerais we came across the two interesting new species of Ambrysinæ described below. As the keys are not supposed to contain descriptions of new species they are described in this paper, with some other data on the systematics of Ambrysinæ in southern Brazil and northern Argentina.

MATERIAL AND METHODS

Measurements are in mm, the length of an eye is measured along its inner margin, its width perpendicularly on its inner margin.

Repositories: MZSP, Museu de Zoologia da Universidade de São Paulo, 01.051 São Paulo, Brazil and NCTN, Nieser Collection, Tiel, The Netherlands

SYSTEMATIC PART

The Ambrysinæ are mainly characterized by the propleura posteriorly meeting medially and covering part of the prosternum. The subfamily has so far only been found in the Americas. They are stream inhabiting insects although one of the best known species, *Ambrysus mormon* Montandon, 1909, may occasionally occur in lakes.

The rank of Ambrysinæ is still under discussion. Some European authors consider them to be a tribus Ambrysinini either in Naucorinae (Popov 1970, Nieser 1975) or in Cryphocerinae (Štys & Jansson 1988, Mahner 1993). American authors on the other hand have a tendency to consider them a separate subfamily Ambrysinæ (Usinger 1941, La Rivers 1971, Polhemus & Polhemus 1988). The cladistic analysis of Naucoridae by Mahner (1993) is unfortunately inconclusive so, somewhat arbitrarily, we decided to follow American usage and consider them a subfamily of Naucoridae.

The Ambryinae contain about 75 species (La Rivers 1971, 1974, 1976) of which only five are not in the genus *Ambrysus* s. l.; two species of *Cataractocoris* in Mexico and Mesoamerica and three of *Carvalhoiella* in South America. The genus *Ambrysus* is richest in Mexico and southwestern U.S.A with about 40 species nearly all endemic to that area. Southern Brasil and northern Argentina together do not badly with 16 species. As there is no identification key available for this region, we prepared one. Combined with the key in Nieser (1975) the Ambryinae fauna of Brazil should be covered.

De Carlo (1935) erected the genus *Melloiella* on the basis of a large species *M. truncaticollis*, with strongly reduced membranes and a characteristic triangular pronotum with straight margins. Otherwise it fits fully into *Ambrysus* and although the other brachypterous species of *Ambrysus* (*A. siolii*) with reduced hemelytra has less reduced membranes, we consider it different at subgeneric level only.

Key to genera and subgenera of Ambryinae

- 1 Fine and dense pilosity on abdominal venter reaching lateral margin (genus *Ambrysus* Stål 1862). 2
- Abdominal venter laterally with a distinct bare shining band. 6
- 2 Metatibia with at least four distinct transverse rows of spines distally, lateral angles of eyes sharply angulate, length 10 mm or more. subgenus *Picrope* La Rivers, 1952
Monotypic: *Ambrysus* (P.) *usingeri* northern part of S. America.
- Metatibia with no more than three transverse rows of spines distally, lateral angles of eyes rounded. 3
- 3 Pronotum obliquely truncate latero-caudally resulting in sharp sub-caudal lateral angles, membrane of right hemelytron of brachypterous form reduced to a narrow strip, macropterous form not known, large species, length over 11 mm subgenus *Melloiella* De Carlo, 1935 stat. n.
Two species in S. Brazil
- Postero-lateral angles of pronotum rounded, membrane of hemelytra well developed even in (rare) brachypterous forms 4
- 4 Hind wing without a costal cell. subgenus *Acytarsus* La Rivers, 1965
Monotypic: *Ambrysus* (A.) *funebis* La Rivers, 1965 California
- Hind wing with a costal cell 5
- 5 Prosternum medially fused to propleura subgenus *Syncollis* La Rivers, 1965
Nine species mainly SW U. S. A. to NW S. America, *Ambrysus* (S.) *teutonius* La Rivers, 1951 in S. Brazil
- Prosternum medio-posteriorly disappearing under the propleura, not fused with them.
subgenus *Ambrysus* Stål, 1861
About 60 species from W. U. S. A. to N. Argentina. Especially rich in species in SW U. S. A. and Mexico.
- 6 Anterior margin of pronotum medially with a distinct and deep excision, punctures dorsally on body with distinct fine granules. *Cataractocoris* Usinger, 1941
Two species, Mexico and Mesoamerica.
- Anterior margin of pronotum medially only shallowly curved caudad, punctures dorsally on body without or with indistinct fine granules *Carvalhoiella* De Carlo, 1963
Three species, S. America.

A second species of subgenus *Melloiella* has been found in Minas Gerais.

Ambrysus (*Melloiella*) *lamprus* sp. n.

(Fig. 1)

TYPE MATERIAL. Holotype brachypterous male (only specimen known) BRAZIL: Minas Gerais, Barragem de Tres Marias, Rio S. Francisco, Feb. 1965, leg. W. Martins (temporarily NCTN, to be transferred to MZSP)

DESCRIPTION. Medium sized flat species, length 11.6, width (across embolium) 7.6, height at level of metacutabula 1.4. Colour yellow with medium brown pattern, rather indistinct on head, pronotum and scutellum, distinct on hemelytra (Fig. 1).

Head, width 2.73, median length 1.80, interoculus anteriorly 0.98, posteriorly 1.40, length of an eye along inner margin 1.20, width of an eye 0.77. Anterior margin of head only slightly projecting in front of labrum (0.05). Labrum semicircular, twice as wide as long (0.55/0.27).

Pronotum, width 6.26, median length 1.65, maximal length (at level of antero-lateral angles) 2.43, length along lateral margin 2.71, lateral margins indistinctly serrate, best visible in ventral view. Postero-lateral angles acute, the smaller more posterior angles also acute (Fig. 2). Propleura fused with prosternum but more elevated than in subgenus *Syncollis*. Scutellum, basal width 3.35, median length 2.04, lateral margins slightly sinuate.

Posterior part of head, pronotum, scutellum and hemielytra except membranes densely beset with fine punctures; those on hemielytra except on embolium each provided with a fine granule.

Hemielytra, reaching apex of abdomen, leaving a distinct strip of connexivum uncovered, without claval suture or nodal furrow, right membrane reduced to a narrow strip, left membrane broader but covered by right hemielytron. Length of claval commissure 2.33.

Caudolateral angles of connexiva 3-6 spinose (Fig. 1); lateral margins distinctly serrate, on segment 4 about 12 serrations/mm.

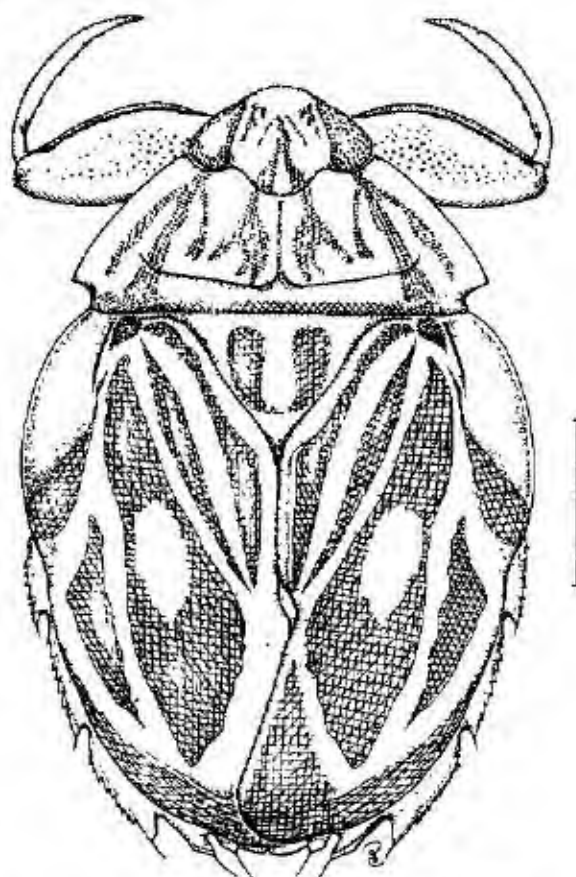


Fig. 1. *Ambrysus (Melloella) lamprus* sp. n. holotype male, habitus (scale 2.5 mm).

Fore leg, femur flattened but broad (L/W 3.1/1.7), tibia 2.5 times as long as tarsus (1.5/0.6). Middle leg, femur six times as long as wide (3.2/0.55), tibia distinctly shorter than femur (2.8) with two transverse apical combs of spines. Hind leg, femur seven times as long as wide (4.0/0.68), tibia longer than femur (4.5) with two apical combs.

Abdominal sternites covered with fine dense pilosity nearly reaching lateral margins.

ETYMOLOGY. *Lamprus*, latinization of Greek *lampros*, splendid or striking, referring to the beautiful dorsal pattern of this species.

COMPARATIVE NOTES. *Ambrysus (Melloiella) lamprus* sp. n. is not very similar to any known species. Its general shape is similar to *A. (M.) truncaticollis* which is, however, distinctly larger (length about 15 mm) and has unicolorous dark hemelytra.

The *Ambrysus* species of the U. S. A. and Central America have been treated by La Rivers (1953) and Usinger (1946), the species of N. Brazil can be identified with Nieser (1975) but there are no recent keys for the comparatively rich fauna of S. Brazil and N. Argentina. With the key below we try to fill this gap.

Key to *Ambrysus* from S. Brazil and N. Argentina

- 1 Metatibia with at least 4 distinct transverse rows of spines at distal end, lateral angles of eyes sharply angulate, length 9–11 mm. Widely distributed in N. Brazil and Guyanas, reaching Mato Grosso. *A. (Picrops) usingeri* La Rivers, 1952
- Metatibia with no more than 3 transverse rows of spines distally, lateral angles of eyes rounded. 2
- 2 Pronotum obliquely truncate latero-caudally resulting in sharp sub-caudal lateral angles, membrane of right hemelytron of brachypterous form reduced to a narrow strip, macropterous form not known, larger species, length over 11 mm (subgenus *Melloiella*). 3
- Postero-lateral angles of pronotum rounded, membrane of hemelytra well developed in (rare) brachypterous forms. 4
- 3 Large species, length about 15 mm, hemelytra except for embolium unicolorous dark, São Paulo, Sta. Catarina, Rio Grande do Sul. *A. (Melloiella) truncaticollis* De Carlo, 1935
- Smaller species, length nearly 12 mm, hemelytra variegated yellow and medium brown, Minas Gerais. *A. (Melloiella) lamprus* sp. n.
- 4 Prosternum and propleura fused, lying in one plane, male lacking the process on left side of tergite 7, Mato Grosso, Sta. Catarina. *A. (Syncolis) teutonius* La Rivers, 1951
- Propleura medially lying ventrally of prosternum (subgenus *Ambrysus*). 5
- 5 Larger species length 10 mm or more. 6
- Smaller species length up to 10 mm. 9
- 6 Median angle of posterior margin of connexivum of segment 6 (at base of operculum) in females with a tooth. 7
- Median angle of posterior margin of connexivum of segment 6 (at base of operculum) in females without a tooth, Argentina: Salta. *A. (Ambrysus) gemignani* De Carlo, 1950
- 7 A relatively broad species, ratio length/width 1.5 (L/W 13/8.5), Central Argentina. Córdoba, Tucumán. *A. (A.) fuscatus* Berg, 1879
- More slender species, length/width 1.8. 8
- 8 Posterior width of pronotum 6.27–6.67mm, body length 13.0–14.2mm, NW Argentina: Jujuy, Salta. *A. (A.) bergi* Montandon, 1897
- Posterior width of pronotum 5.96–6.27mm, body length 11.9–13.2mm, Central Argentina: Córdoba, San Luis; ? Bolivia. Remark: *A. bergi* and *A. ochraceus* are very similar, see Lopez Ruf (1993) who also doubts the occurrence of *A. ochraceus* in Bolivia in view of distribution in Argentina. *A. (A.) ochraceus* Montandon, 1909
- 9 Caudolateral angles of connexiva 4 & 5 (3 & 4 visible) distinctly spinose. 10
- Caudolateral angles of connexiva 4 straight, of connexiva 5 with a small spine. Only known by the holotype from Pernambuco, the better known *A. stali* La Rivers from Guyanas, Pará and N. Amazonas may be a subspecies of *A. obscuratus* (Nieser 1975). *A. (A.) obscuratus* Montandon, 1898
- 10 Claval suture absent, hemelytra not reaching apex of abdomen but membranes well developed, broad margin of connexiva exposed, head (except eyes), pronotum, scutellum, embolium and connexiva (except for small dark

- spot anteriorly) yellow, hemelytra blackish (except ill defined V-shaped yellowish spot apically on corium), southern part of Pará, only 4 specimens all brachypterous are known, the macropterous form will probably be recognizable by its variegated pattern *A. (A.) stali* De Carlo, 1966
- Claval suture present, hemelytra reaching or nearly reaching the apex of abdomen, exposed area of connexive narrow. 11
- 11 Pronotum anteriorly with a distinct median depression (not the incision but in dorso-vertical direction), comparatively broad oval shape, length 8.5 mm, width 5.2 mm. Argentina: Corrientes, Misiones. *A. (A.) acutangulus* Montandon, 1897
- Pronotum anteriorly without median depression, rather narrowly oval shape, length 8.2 mm, width 4.5 mm. 12
- 12 Antero-lateral angles of pronotum narrow (but not pointed), lateral margins of pronotum finely crenulate-serrate, Mato Grosso: Cuiabá. *A. (A.) fraternus* Montandon, 1897
- Antero-lateral angles of pronotum obtuse, lateral margin not serrate, ? Minas Gerais: Ouro Preto. Montandon 1897 gives Villa Rica, Brésil. De Carlo 1950 supposes this is in Paraguay but it probably refers to Vila Rica de Ouro Preto which until 1897 was the capital of Minas Gerais. *A. (A.) attenuatus* Montandon, 1897

The genus *Carvalhoella* contains two species, we can add a third collected in SW Minas Gerais, closely related to *C. beckeri* De Carlo which is also from Minas Gerais.

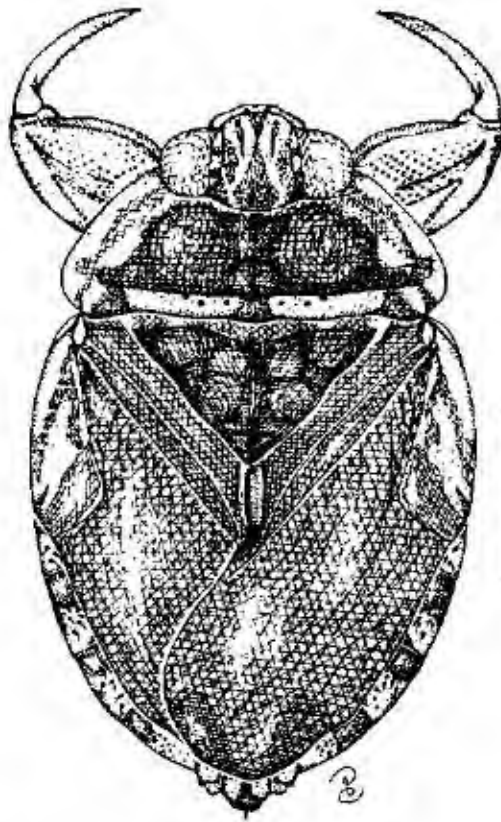


Fig. 2. *Carvalhoella stysi* sp. n. holotype female, habitus (scale 2.5 mm).

***Carvalhoiella stysi* sp. n.**
(Figs 2–3)

TYPE MATERIAL. Holotype female and 2 female paratypes, all macropterous, BRAZIL. Minas Gerais, São Roque, at foot of waterfall at NE edge of Serra da Canastra (20° 15' 12" S, 46° 24' 24" W), pool and beginning of stream, one specimen from narrow crevices in wet rock behind the waterfall, current in pool virtually zero, in stream variable, leg. N. Nieser & A. Pelli (N9637) (NCTN).

DESCRIPTION. Medium sized species, length 10.1–10.7, width (across embolium) 6.7–6.8. Colour dark brown, with lateral margins of pronotum, embolium, connexivum and legs yellowish.

Head, width 2.90–3.05, median length 1.75–1.82, interoculus anteriorly 1.17–1.22, posteriorly 1.42–1.52, length of an eye 1.27–1.32, width of an eye 0.80–0.87. Anterior margin of head only slightly projecting in front of labrum (0.1). Labrum two thirds long as wide (0.4/0.6), apex bluntly rounded.

Pronotum, width 5.7–5.9, median length 1.70–1.86, maximal length (at level of antero-lateral angles) 2.50–2.60, length along lateral margin 2.73–2.78, lateral margins smooth. Postero-lateral angles rounded (Fig. 2). Propleura lying over prosternum not fused medially. Scutellum, basal width 3.75–3.90, median length 1.80–1.85, lateral margins slightly sinuate.

Head, pronotum, scutellum and hemelytra except membranes and lateroposterior art of embolium densely beset with fine punctures each provided with a very small indistinct granule.

Hemelytra, reaching apex of abdomen, leaving a distinct strip of connexivum uncovered, claval suture and nodal furrow distinct, membranes well developed. Length of claval commissure 0.95–1.01; length of embolium 3.1–3.2, greatest width of embolium 1.0–1.1.

Outer margin of connexiva virtually continuous and smooth (non-serrate), caudolateral angles of connexiva truncate or slightly rounded except for segment five which has a very short blunt spine contiguous with the outline of abdomen.

Fore leg, femur swollen and broad (L/W 2.3/1.9), tibia four times as long as tarsus (1.6/0.4), claws absent. Middle leg, femur four times as long as wide (2.7/0.7), tibia distinctly shorter than femur (2.7/2.2) with two transverse apical combs of spines. Hind leg, femur four and a half times as long as wide (3.3/0.7), tibia slightly longer than femur (3.6/3.3) with two apical combs of spines.

Abdominal sternites covered with fine dense pilosity, a broad median band and broad margin laterally on connexiva bare. Female lateral margin of sternite 7 concave, genital operculum apically shallowly incised with a pair of small sublateral swellings (fig. 3).

ETYMOLOGY. Named for Prof. Dr Pavel Štys for his contributions to the knowledge of Heteroptera. Comparative notes, see key below.

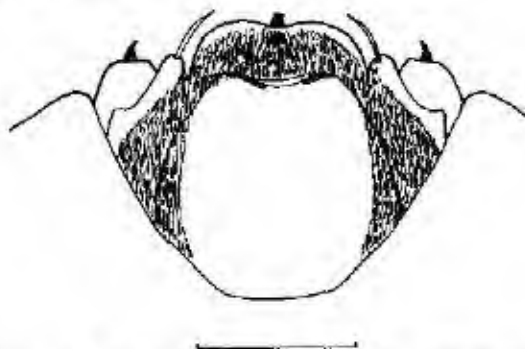


Fig. 3. *C. stysi* sp. n. paratype female, apex of abdomen in ventral view (scale 1.0 mm)

REMARK Nieser (1975) placed *Carvalhoiella* in Naucorinae mainly because De Carlo (1963) does not mention some important characteristics of Ambrysininae in his description of the genus. After studying actual specimens we conclude that the genus should be in Ambrysininae after all, especially in view of the prosternal structure.

Key to the species of *Carvalhoiella*

- | | |
|-----------------------------------------------------------------------------------|----------------------------------|
| 1. Smaller species, length 8.5 mm, dorsum smooth and shiny, Surinam | <i>C. nuda</i> La Rivers, 1976 |
| – Larger species, length 10 mm or more, dorsum punctate and dull | 2 |
| 2. Length 12 mm, female operculum apically straight, Brazil: Minas Gerais | <i>C. beckeri</i> De Carlo, 1963 |
| – Length less than 11 mm, female operculum apically concave, Brazil: Minas Gerais | <i>C. styti</i> sp. n. |

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Does the architecture of lateral pterothoracic region and thoracico-abdominal junction in the Notonectidae, Pleidae, and Helotrephidae (Heteroptera: Nepomorpha) reflect phylogenetic relationships?

Miroslav PAPÁČEK

University of South Bohemia, Pedagogical Faculty, Jeronýmova 10,
CZ-37115 České Budějovice, Czech Republic

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Abstract. The lateral thoracico-abdominal regions of thirty species of thirteen genera of the families Notonectidae, Pleidae, and Helotrephidae (*Notonecta* L., 1758, *Euhares* Spinola, 1837, *Aphelonecta* Lansbury, 1965, *Nychia* Stål, 1858, *Mariaregia* White, 1879, *Anisops* Spinola, 1837, *Buenoa* Kirkaldy, 1904, Pleidae: *Plea* Leach, 1817, *Paraplea* Esaki et China, 1928, Helotrephidae: *Helotrephes* Stål, 1858, *Distotrephes* Polhemus, 1990, *Idiotrephes* Lundblad, 1933, *Trephotomas* Papáček, Štys et Tonner, 1988) were studied. A simple method for generalization of architecture of the studied body region was developed. This method is usable for valid comparison of main structures, for study of their origin and anagenetic changes. The morphological features of the pterothorax and basal abdominal region are partly influenced by the locomotion, feeding and respiratory strategies, and by the pteropolymorphism too. Nevertheless, they have significant differences on the taxonomic level of tribes, subfamilies and families. Some anagenetic trends of the arrangement of the lateral pterothoracic region and the thoracico-abdominal junction were ascertained in the particular taxa. A hypothesis on the origin and homologization of the individual parts of the thoracico-abdominal junction was expressed.

Morphology, pterothoracic pleura, thoracico-abdominal region, phylogeny, anagenetic trends, classification, aquatic Heteroptera, Notonectidae, Pleidae, Helotrephidae

INTRODUCTION

Aquatic bugs are often used as a model group of true bugs for various kinds of ecological, physiological and morphological studies. Special attention has been paid to the study of the morphology of its ventrolateral thoracic region and the base of abdomen. The results of studies of these body regions have been summarized by Papáček (1987) and Papáček et al. (1990). The reason for attention, that is paid particularly to these body regions, is that they are functionally important for respiration and their architecture reflects some life strategies too.

This research was concentrated on looking for the main characters of the formation of the lateral pterothoracic and thoracico-abdominal body region in three families of aquatic bugs, which are accepted as phylogenetically closely related (see e. g. Schuh & Slater 1995). Margaret C. Parsons (1974), the author of today already classic but still up to date studies about this region of exoskeleton in water bugs, studying thirteen species of Naucoroidea, found that in the morphology of studied area there exist certain inter- and intragenetic differences. She came to a conclusion that the modifications of pterothoracic pleura did not reflect the phylogenetic relationships but are partly functional adaptations. It is quite possible that exclusive pterothoracic and thoracico-abdominal architecture has never been used for any studies on the phylogeny of Nepomorpha for this reason. Nevertheless, Mahner (1993) have used some particular characters of this body region for his study of phylogenetic relationships in nepomorphan bugs. Ammorim et al. (1996) stated that thoracic

sclerites presented useful information for concerning the discussion about the phylogenetic relationships among the basal stems of Diptera. Author of presented study supposed the pterothoracic and thoracico-abdominal architecture reflects the phylogenetic relationships between an individual taxa (especially between taxa higher than the genera) in Nepomorpha. It is a question, what characters and what level of generalization should be used for morphological comparison of individual structures and for the judgement of phylogenetic relationships.

The following main questions were put. (1) How is the thoracico-abdominal junction formed in individual taxa? (2) Is it possible to homologize the thoracico-abdominal sclerite which has an unclear origin? (3) Is it possible to define the individual taxa through the mediation of the architecture of the studied body region? If so – on what taxonomic level? (4) What anagenetic trends in the architecture of this body region are expressed in the Notonectidae, Pleidae and Helotrephidae?

MATERIAL AND METHODS

Material examined

Notonectidae. Notonectinae: Notonectini: *Notonecta glauca* L., 1758, *N. lutea* Müller, 1776, *N. viridis* DeGeer, 1909, (all from Central Europe, Czech Republic), *N. undulata* Say, 1832 (from North America, Canada), *Euthares ciliata* (Fabricius, 1798), *E. sinica* (Stål, 1854) (both from Southeast Asia, Vietnam), *E. sobria* (Stål, 1855) (from Northeast Africa, Ethiopia), *E. woodwardi* Lansbury, 1968 (from Southwest Australia, Victoria), *Aphelonecta gavin* Lansbury, 1966 (from Southeast Asia, Vietnam) (all specimens with hindwings of macropterous type (= macr.)). Nychiini: *Nychia limpida* Stål, 1860 (hindwings of micropterous type (= micr.)) (from Northeast Africa, Sudan), *Martarega membranacea* White, 1879, *M. gonostyla* Truxal, 1949 (both from South America, Guyana), *M. houdrenensis* Baro, 1932 (from Central America, Panama) (all specimens of *Martarega* spp. with hindwings of brachypterous type (= brach.)). Anisopinae: *Anisops sardus sardus* Herrich-Schaeffer, 1849 (from Southeast Europe, Turkey, macr.), *A. breddini* Kirkaldy, 1904, *A. bouvieri* Kirkaldy, 1904 (both from Southeast Asia, Vietnam, macr., and brach.), *A. nasutus* Fieber, 1851 (from Southeast Asia, Vietnam, and North Australia, Northern Territory; macr., and brach.), *A. thienemanni* Lundblad, 1933 (from Southwest Australia, Victoria, brach.), *Buenoa nitida* Truxal, 1953, *B. incompta* Truxal, 1953 (both from South America, Guyana, brach.), *B. gracilis* Truxal, 1953 (from Central America, Mexico, brach.).

Pleidae. *Plea minutissima* Leach, 1817 (from Central Europe, Czech Republic, macr.), *P. (Neoptea) striola* (Fieber, 1844) (from North America, USA, Connecticut, micr.), *Paraplea indistincta* (Matsunura, 1905) (from Southeast Asia, Vietnam, macr., and micr.), *Paraplea pulhula* (Stål, 1855) (from Africa, Sudan, micr.).

Helotrephidae. Helotrephinae, Helotrephini: *Helotrephes semiglobosus* Stål, 1860 (macr., and micr.)¹, *Limnotrephes* *Distotrephes* *stys* Polhemus, 1990 (micr.), *Idiotrephes chinai* Lundblad, 1933 (macr., and micr.)², *I. maur* Papáček, 1994 (micr.). Trephotomasinae: *Trephotomas compactus* Papáček, Stys et Tenner, 1988 (micr.) (all helotrephid spp. from Southeast Asia, Vietnam).

Methods

The material was preserved in 70% ethanol, some specimens in Bouin's fixative, and dissected in 96% ethanol under a stereoscopic microscope. Soft tissues were hand-removed, using watchmaker forceps since clearing in lactic acid, tended to hand using a sharp razor blade. Separated parts of exoskeleton were mounted in Euparal or Eukitt for microscopic examination. For SEM examination the specimens were lyophilized in a Leybold-Heraeus apparatus, coated with a gold-palladium mixture in a Pollaron apparatus, and studied and photographed under stereoscopic microscope. The real characters of individual model species, as well as the main structures presented in generalized figures (see below), were compared and analyzed.

Terminology, figures, method of generalization, abbreviations

The morphological terminology used here is partly summarized in abbreviations and in Fig. 1, and derived mainly from Papáček (1987) and Parsons (1970, 1974, 1976). Not all of names, established by Mahner (1993, p. 140) in his classification, are used here, for the reason of their nomenclatural uncorrectness (see also Andersen (1995)). Superfamilies Notonectoidea and Pleoidea are accepted sensu Stys & Jansson (1988).

¹ Material is still taxonomically revised by H. Zettl at present.

² Material is still taxonomically revised by M. Papáček and H. Zettl at present.

All figures represent strongly schematized lateral views (level of generalization compare figs – see Papáček (1987), Papáček et al. (1990) and Parsons (1970)) on the pterothoracic and basal abdominal body regions. The figures have been developed in four steps: (1) making SEM photography, (2) drawing the realistic figure with countours of individual structures by SEM photography, (3) drawing the generalized schematic figure with simplified shapes of structures (general shapes, angles and proportions fully preserved), (4) transformation of all figures in the same relative scale. Differently lined or dotted areas show the attachment of the structure to the different body segments (see Fig. 1 Model architecture in Insect) – exclude of Fig. 2. Level of generalization eliminates morphological differences between macro- (brachy-) and micropterous morphs of the same species (cf. e.g. Larsén (1950)).

Abbreviations on the figures: CX – metacoxa, DLT – dorsal laterotergite, EM – epimeron, ES – episternum, LT – laterotergite, PN – postnotum, S – spiracle, SU – scutum, T – tergite, TAM – functional thoracico-abdominal membrane, TAS – thoracico-abdominal sclerite, VLEM – ventral and lateral lobe of mesothoracic epimeron, VLES – ventral and lateral lobe of metathoracic episternum, VLT – ventral laterotergite, W – wing, WAK – wing anchoring knob of mesothoracic epimeral lobe, (WAK_m – wing anchoring knob of metathoracic epimeron, WAK₂ – wing anchoring knob of anterolateral projection of the second abdominal segment). The Roman numerals II, III show the attachment of the structure to the meso- or metathorax. The Arabic numerals 1, 2 show the attachment of the structure to the first or second abdominal segment.

Cladistic analysis

Main comparable characters which appear in all studied groups were found. These characters are two- or three-state. Three-state characters are treated as ordered. The data matrix was polarized by the hypothetical groundplan of water bugs, deduced from results of Parsons (1974). Individual groups, which can be defined by complex characters, were put in data matrix. Taxa, which have homogenous morphology of studied body regions and which are not subdivided to the tribes – family Pleidae, subfamilies Anisopinae, and Trophotomasiinae – were treated as groups, which are hypothetically equivalent to the taxonomic level of tribes. The Hennig86, Version 1.5 by Farris (1988) and the Random Cladistic software package by Siddall (1995) were used for cladistic analysis.

RESULTS AND THEIR DISCUSSION

1. Architecture in Nepomorpha

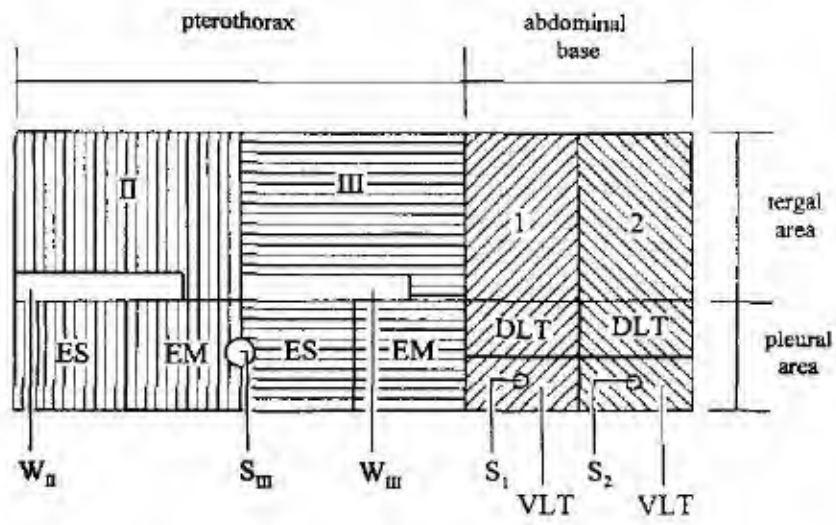
Architecture of dorsopleural pterothoracic and thoracico-abdominal region of the exoskeleton in pterygote insects was explained by Snodgrass (1927). It is illustrated by Fig. 1. Model architecture of these body regions in Nepomorpha, which represents probably ancestral nepomorphan situation is somewhat derived (e. g. Parsons (1974) and Papáček (1987), see also Fig. 1). The main common characters – synapomorphies – of the all nepomorphan families are following:

- (i) Mesepimeron and metepisternum expand into large lobes (VLEM, VLES).
- (ii) Lateral mesepimeral lobe projects into dorsally oriented forewing anchoring knob.
- (iii) Metepimeron is a relatively small sclerite which merges posteroventrally to the thoracico-abdominal sclerite (TAS – see also Fig. 2). (Note: The origin of TAS is unclear. According to Larsén (1945) it is a derivate of the first abdominal sternum. According to Parsons (1974) it is a metathoracic origin.)
- (iv) The membranous area (= thoracico-abdominal membrane, TAM) represents the dorsolateral thoracico-abdominal junction. TAM is formed partly by unsclerotized portion of the first abdominal tergite and partly by the membrane between the first and the second abdominal segment. It has a different extent in the various representatives of aquatic bugs.
- (v) The anterior pleural projection of the second abdominal segment (formed by laterotergites – see also Fig. 2) is shifted anteriorly in the metathoracic area. It represents ventrolateral slack thoracico-abdominal junction.

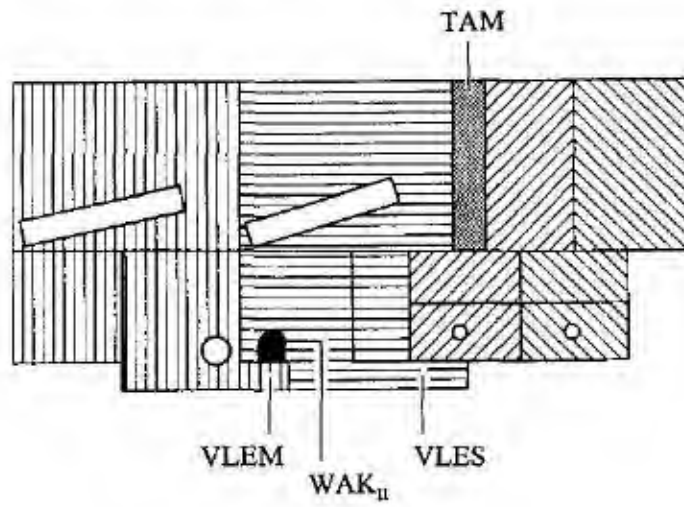
2. Generalized architecture in the Notonectidae, Pleidae, and Helotrephidae

The basic situation, which is only relatively slightly derived from ancestral nepomorphan model, is probably represented by the architecture in Notonecta, Notonectini respectively. Pterothoracic, and thoracico-abdominal region in Notonectini, have a lot of characters (symplesiomorphies),

MODEL ARCHITECTURE IN INSECTA



MODEL ARCHITECTURE IN NEPOMORPHA



which correspond to the characters in generalized model of Nepomorpha (cf. Figs 1, 3, see also characters (i) – (v) in previous text). The opinion about most primitive situation in Notonecta among the Notonectidae can be supported also by conclusions of Papáček & Štys (1985).

The tendency towards the shift of lateroventral region of the abdominal base to the metathoracic region in metacoxal area is apparent in all studied species. This tendency is related with the different degree of reduction or with other modifications of the first abdominal segment. The three modifications of the dorsolateral thoracico-abdominal junction were ascertained.

- (1) The first mediotergite is joined with the metathorax by a narrow functional thoracico-abdominal membrane (Notonectini).
- (2) The first mediotergite is desclerotized and reduced in a different degree, the functional thoracico-abdominal membrane is relatively extensive (Nychiini, Pleidae, Helotrephidae). This modification of junction has several variants, which are specific on the taxonomic level of tribes (see below and also Figs 3, 4).
- (3) The first mediotergite is fused with the metathorax (Anisopinae). Dorsolateral part of thoracico-abdominal membrane is not formed.

Lateral part of metathoracic pleura and thoracico-abdominal region (especially metepimeron, thoracico-abdominal sclerite and membrane surrounding the first abdominal spiracle), has a tendency to shift and invaginate ventromedially. Air chamber of the first abdominal spiracle is formed and relatively expanded by this way (see also below). The basic situation and modifications of them are apparent from the Fig. 2.

Different degrees of the fusion of the metathorax with abdomen, same as the the position of thoracico-abdominal sclerite and the angle between the metapleural sulcus and the lengthwise body axis, can help to explain the homologization of structures which origin is unclear.

- (1) The thoracico-abdominal sclerite is a remnant of the (dorsal) laterotergite of the first abdominal segment
- (2) The upper portion of the membrane between the thoracico-abdominal sclerite and the metacoxa (metacoxal membrane) is a desclerotized rudiment of the (ventral) laterotergite of the first abdominal segment.

These conclusions can be supported by further argumentation. In Anisopinae the thoracico-abdominal sclerite is connected with the first abdominal tergite (an argument if it is a primary situation). Not only in Notonectoidea and Pleoidea but in most Nepomorpha there undoubtedly exists the tendency towards the shift of the ventrolateral region of the abdominal base to the metathoracic region (see also Papáček (1987), Papáček et al. (1990), Parsons (1970, 1974, 1976). The second up to eight abdominal spiracles of aquatic bugs lie in the ventral laterotergal region. Cobben (1978) found an intrasegmental position of the first abdominal spiracle in the first nymphal instar of *Plea minutissima*. It means such a position which still corresponds with the position of the other abdominal spiracles. We can assume, that in the ontogenetic/anagenetic process not only the spiracle is being shifted but together with also the "mother sclerite" – i.e. a laterotergite, which can partly or fully desclerotize, merge with others, etc. The assumption, that both the spiracle and the surrounding cuticular region are shifted, is supported by the correlation found in Notonectidae – the correlation of the size and of the angle between the metapleural sulcus and the longitudinal body axis and the extent of the thoracico-abdominal sclerite and the position of the first

Fig. 1. Generalized (model) architecture of dorsopleural pterothoracic region and thoracico-abdominal junction in pterygote Insect (according to Snodgrass (1927)) compared with generalized architecture of the same body region in Nepomorpha (by Papáček (1987) and Parsons (1974)). Both figures are strongly generalized and schematized. Lettering – see in the chapter Material and methods.

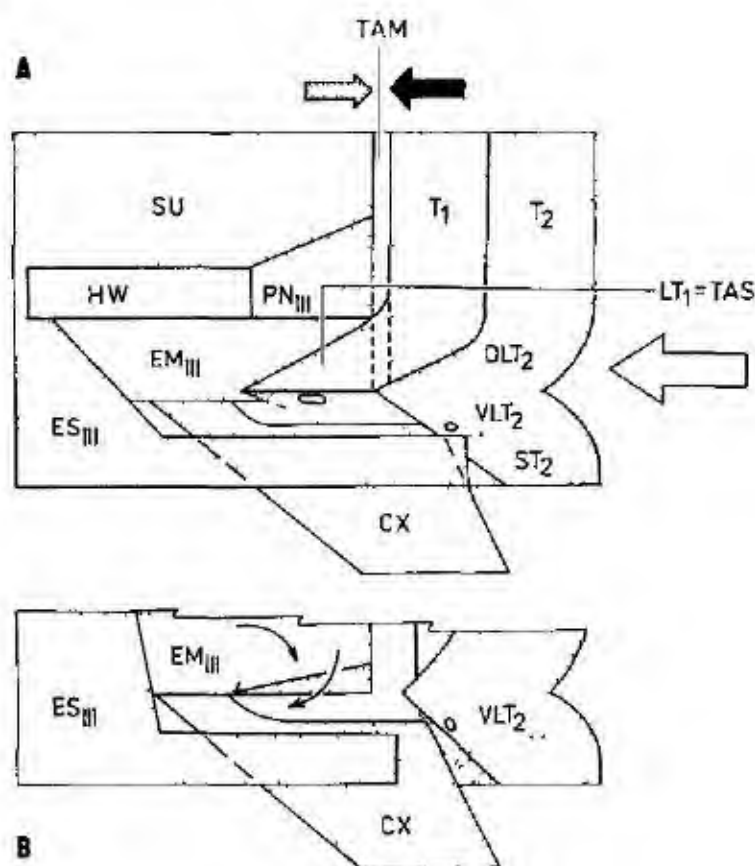


Fig. 2. Generalized architecture of the dorsopleural pterothoracic and thoracico-abdominal junction in the Notonectidae, Pleidae, and Helotrephidae. Homologization of thoracico-abdominal sclerite.

A — the basic scheme and its individual variants. The white large arrow shows the tendency towards the shift of the lateroventral and ventral regions of the abdominal exoskeleton to the metathoracic region. The dotted arrow shows the tendency of the desclerotization of the first and second medioclergite respectively, and the formation of extensive functional thoracico-abdominal membrane in the Notonectinae (Notonectidae), Pleidae, and Helotrephidae. The black arrow indicates an opposite tendency — the tendency towards merging the first abdominal tergite with posterior metathoracic edge and sclerotization of the "border region" in the subfamily Anisopinae (Notonectidae). Different degrees of the "fusion" of the metathorax with abdomen, same as the position of thoracico-abdominal sclerite and the angle included by the metapleural sulcus with the lengthwise body axis, can help to explain the homologization of structures, which origin is unclear.

B — the derived situation in Nychitini (Notonectidae) and Pleoidea (presented only lateral part of the metathoracic pleuron and lateroventral basal abdominal region). The upper arrow represents the direction of the metapleural sulcus and the shift of the thoracico-abdominal sclerite in comparison with the situation in Notonectini. The bottom arrow shows the direction of invagination of the supracoxal membrane, and the first abdominal spiracle under the thoracico-abdominal sclerite.

abdominal spiracle. The larger the angle, the "lower" the thoracico-abdominal sclerite, and the more ventrally situated spiracle.

3. Specific features of architecture in families studied

3.1. *Notonectidae*

Formation of body region studied differs each from other on the taxonomic level of tribes or subfamilies respectively (Fig. 3).

Main characters

Notonectinae, Notonectini. The first abdominal mediotergite is clearly separated from the metathorax. The extent of the thoracico-abdominal membrane is variable. The thoracico-abdominal sclerite is well subdivided. The membranous supracoxal region is wide, the first abdominal spiracle is in the "high" lateral position. The rudiment of metepimeral wing anchoring knob, is developed in *Aphelonecta*, but the other major characters is the same as in *Notonecta* and *Enithares*. Zettel (1993) stated that the genus *Aphelonecta* is closely related to *Enithares* and synonymized the tribus Aphelonectini with the tribus Notonectini. The findings of this presented study confirm the Zettel's conclusion.

Notonectinae, Nychiini. Metathorax and abdomen are separated by an extensive thoracico-abdominal membrane. The thoracico-abdominal sclerite is only narrow (*Martarega*) or absent (*Nychia*). (It is rather reduced than amalgamated with surrounding sclerites.) The first abdominal spiracle lies ventrally. The anterior projection of the second abdominal segment does not reach the metathorax. **Anisopinae.** The first and second abdominal tergites merge with the metathorax. The dorsolateral portion of thoracico-abdominal membrane is absent. The thoracico-abdominal sclerite smoothly changes posteriorly into the first abdominal tergite (mediotergite). The first abdominal spiracle lies in the "low" lateral position. The anterior projection of the second abdominal segment is overlapped to the metepisternal lobe.

Anagenetic trends

Two opposite trends appear in Notonectidae. Desclerotization of dorsal portion of the thoracico-abdominal junction (development of TAM) in Notonectinae, and sclerotization of this region and development of the tight thoracico-abdominal junction in Anisopinae. Two opposite ways of evolutionary processes were also undoubtedly connected with the evolution of the different predatory strategies and adaptation on the ecological niches of representatives of the individual taxa. The next main trend is the shift of the posteroventral metathoracic area more ventrally. It appears in three different degrees: Notonectini (most dorsal position) → Anisopinae → Nychiini (most ventral position).

3.2. *Pleidae*

The architecture of body region studied is uniform in the all examined species (Fig. 4). The fact closely corresponds to the simple classification of the family.

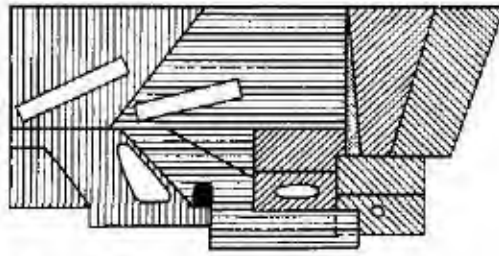
Main characters

The first abdominal segment is dorsolaterally totally desclerotized, it forms thoracico-abdominal membrane. The dorsal portion of the second abdominal segment is also membranous and it is incorporated into thoracico-abdominal membrane too. Thoracico-abdominal sclerite and first abdominal spiracle are shifted and invaginated ventrally. Metepisternal lobe overlaps the anterior projection of the second abdominal segment (tight boundary). There exists a strongly developed, forewing coaptative apparatus. It is formed by (1) knob of mesepimeral lobe which fits into a fovea in the embolus margin of the forewing (WAK_{II}), (2) an anterolaterally pointing metepimeral knob

NOTONECTIDAE

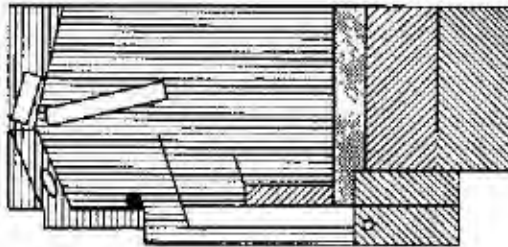
Notonectinae

Notonectini *



* *Aphelonecta* - with WAK_{22}

Nychiini



Anisopinae

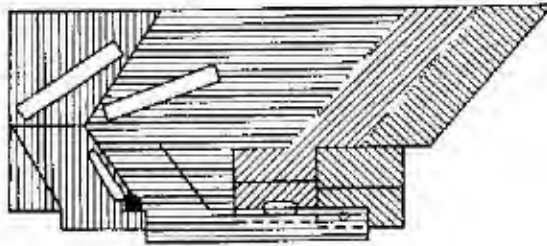


Fig 3 Lateral pterothoracic region and thoracico-abdominal junction in Notonectidae

which fits into a fovea on the internal surface of corium (WAK_{dl}), (3) dorsal knob of anterior projection of the second abdominal segment which fits into a posterior fovea in the embolus margin (WAK_2).

Anagenetic trends

Three evident trends were ascertained. Desclerotization of the basal abdominal segments in dorsolateral portion, a shift of thoracico-abdominal sclerite and first abdominal spiracle ventrally, and an extreme development of the forewing-anchoring apparatus.

3.3. Helotrephidae (Helotrephini and Trephotomasinae)

Formation of studied body region differs each from the other on the taxonomic level of tribes or subfamilies respectively (Fig. 4). There exist closely relationships between Helotrephini and Limnotrephini.

Main characters

Helotrephinae, Helotrephini. Second abdominal tergite is separated from the metathorax by extensive thoracico-abdominal membrane. The whole first tergite is a portion of this membrane. Metepisternal lobe overlaps the anterior projection of the second abdominal segment (tight boundary). Thoracico-abdominal sclerite is very narrow but laterally visible. First abdominal spiracle lies ventrally. Wing-anchoring apparatus is formed only by two knobs (WAK , WAK_{dl}).

Helotrephinae, Limnotrephini. Limnotrephini differs from the Helotrephini by following main characters. Mesepimeron is anteriorly projected into a small lobe. Metepisternal lobe does not overlap the anterior projection of the second abdominal segment. The intersegmental sulcus between meso- and metathorax is compressed more anteriorly, but metepimeral wing-anchoring knob is localized more posteriorly.

Trephotomasinae. Trephotomasinae differs from the Helotrephinae especially in a long mesepimeral lobe, which is projecting in the area of the first abdominal segment, by ventral shift of thoracico-abdominal sclerite (It is not visible laterally), and by the anterior compression of the pterothorax, which is undoubtedly connected to the anterior shift of both the basal abdominal sclerites (both are well sclerotized). The wing anchoring apparatus is formed only by one knob (WAK_l). It is probably the primary state.

Anagenetic trends

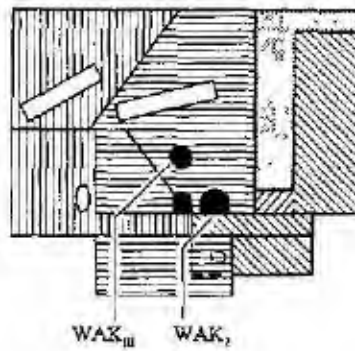
The relative shortening of pterothorax, desclerotization of large areas of one or both abdominal tergites, and ventral shift of thoracicoabdominal sclerite related with ventral shift and invagination of the first abdominal spiracle – they are the main evolutionary trends or tendencies characteristic for the all studied species of Helotrephidae. Two last mentioned trends are common (synapomorphic) for Pleoidea (both Pleidae and Helotrephidae).

4. Characters polarity and cladistic analysis

The fifteen characters listed below and their states are summarised in matrix (see Table 1; ordination – see in Material and methods).

1. pterothorax is longer than its high (0), is shorter than its high (relative shortening of pterothorax) (1)
2. mesonotum is approximately the same length as metanotum (0), is shorter than metanotum (1)
3. ventrolateral mesepimeral lobe does not reach the thoracico-abdominal sclerite (short) (0), reaches the level of thoracico-abdominal sclerite (1), reaches the level of thoracico-abdominal membrane (long) (2)
4. ventrolateral metepisternal lobe laterally overlaps anterolateral abdominal projection (0), reaches this projection (1)

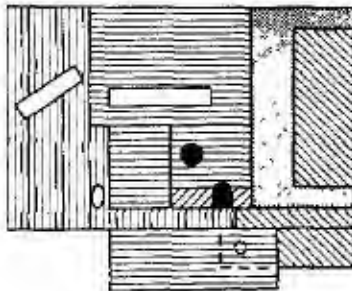
PLEIDAE



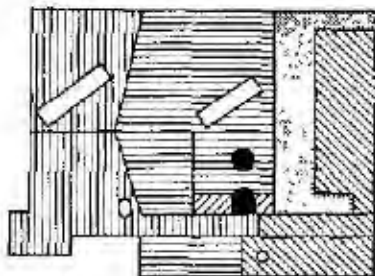
HELOTREPHIDAE

Helotrephinae

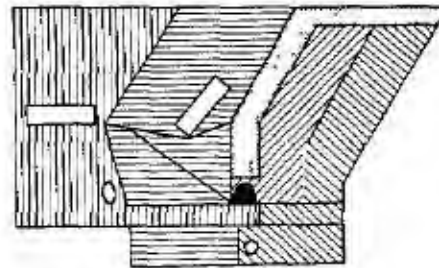
Helotrephini



Limnotrephini



Trephotomasinae



Idiocorinae ?

Neotrephinae ?

Fischerotrephinae ?

Fig. 4. Lateral pterothoracic region and thoraco-abdominal junction in Pleidae, and some Helotrephidae (Helotrephinae, Trephotomasinae).

5. ventrolateral lobe of metepisternum is distinctly longer than its lateral portion (0), is somewhat longer (1)
6. metepimeron is rectangular (0), subtrapezoidal (1), triangular (2)
7. presence of wing anchoring knobs: mesepimeral knob (WAK_{III}) (0), mesepimeral and metepimeral (WAK_{III}) knobs (1), mes- and metepimeral knobs, and knob of the anterolateral projection of the second abdominal segment (WAK₂) (2)
8. metathoracic spiracle is large, elongated, in the lateral position (0), small, rounded, in the ventrolateral position (1)
9. thoracico-abdominal sclerite is well developed (0), somewhat reduced (1), invaginated (no visible) (2)
10. first abdominal spiracle is localized in the lateral position (0), in the ventrolateral position (1), in the ventral position (2)
11. anterolateral projection of the second abdominal segment reaches anteriorly the metathorax (0), does not reach the metathorax (1)
12. presence of the functional thoracico-abdominal membrane (0), its absence (first abdominal mediotergite is fused with metathorax) (1)
13. extent of the functional thoracico-abdominal membrane: narrow (0), large (1), large, continued with medial desclerotization of the first or first-two-three mediotergites (2)
14. first abdominal mediotergite is preserved (0), reduced (1)
15. first two mediotergites are fully separated (0), partly fused (1), fully fused (2)

Presented cladistic analysis has only phragmentary character. Only genera *Anisops* and *Buenoa* were studied from subfamily Anisopinae. Not enough of material of Neotrepinae, Idiocorinae and Fischerotrephinae (Helotrephidae) (cf. Mahner (1993), and Zettel (1994)) was available. Anyway, it is necessary to have in mind, that the aim of this study is not the revision of classification, but to give answers (1) if any taxons can be defined by characters of thoracico-abdominal pleura, and (2) if these characters are usable for the judgement of phylogenetic relationships. My opinion is, that for these purposes the phragmentary analysis could be accepted.

The lowest taxa that can be defined by the complex of main structural characters of studied body regions, were examined by cladistic analysis (Pleidac, Anisopinae, Trephotomasinae – see in Material and methods). Analysis was based deliberately only on fifteen characters of thoracico-abdominal pleura. Its results are two alternative parsimonious 28 steps long trees (ci = 78, ri = 80) and one consensus tree. Their topology and boot strap values are apparent from the Fig. 5.

Tab. 1. Group (tribe) character matrix of Notonectidae, Pleidac and some Helotrephidae. Meaning and states of characters are explained in text. (Hierarchic classification – see Mahner (1993: 48, 140, 143, 151).) * – tribus is not established or its establishment is doubtful (Anisopinae); ? – state of character is not possible to determine; – – character absent

Character No	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Notonectini	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
Nychiini	0	1	0	1	0	1	0	0	1	2	1	0	1	0	1
Anisopinae*	0	1	0	0	0	1	0	0	0	1	0	1	–	0	2
Pleidac*	1	1	1	0	0	1	2	1	2	2	0	0	2	1	?
Helotrephini	1	1	1	0	0	0	1	1	1	2	0	0	2	1	?
Limnotrephini	1	1	1	1	0	0	1	1	1	2	0	0	2	1	?
Trephotomasinae*	1	0	2	1	1	2	0	1	2	2	0	0	2	0	1

If we compare these cladograms (Fig. 5) with Mahner's (1993, pp. 48, 140, 143, 151) classification corrected by data of Zettel (1993, 1994) on Fischerotrephinae (Helotrephidae), we can with a certain probability expect certain differences. Each of these classifications is surely based on the analysis of a different data set. Nevertheless, from this comparison it is possible to come to some conclusions and formulate to some problems.

The tribe Notonectini has the most plesiomorphic character within the Notonectoidea (see also Papáček & Štys 1985). Mahner (1993, p. 139) says that his classification of Notonectinae is problematic. His cladogram (p. 140) is not complete. Relationships between Notonectini (Aphelonectini?), and Nychiini are not expressed there. Here presented trees, based only on one-sided analysis, indicate the possible relations of these tribes and the subfamily Anisopinae, and makes an alternative to the cladogram of Mahner (1993). It shows that the "group" Nychiini could be considered as a separate taxon out of subfamily Notonectinae. Alternative trees point at close relationships between Pleidae and Helotrephinae, but corresponding lines are the clades of a relatively low support. Paraphyly of Helotrephidae expressed here, based on the position of Trephotomasinae, is surprising. It is evident from the topology of both cladograms (presented and Mahner's), and from Zettel's (1997) discussion on possible phylogenetic relationships of Idiocorinae and Limnotrephini, that the cladistic justifying of hierarchic classification of Pleoidea needs a more

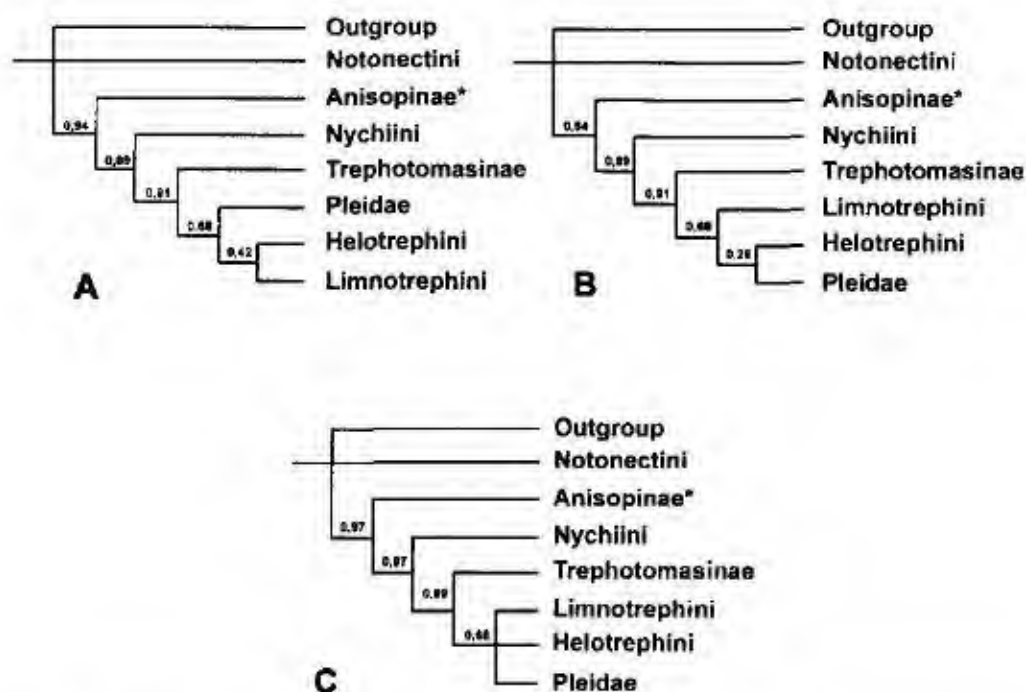


Fig. 5. Fragmentary cladograms of some taxa of Notonectidae, Pleidae, and Helotrephidae based on analysis of 15 characters of the pterothoracic pleuron and thoraco-abdominal junction. A, B – alternative trees, C – consensus tree. Anisopinae* – *Anisops* and *Buenoa* only.

precise study of the structural characters (including the architecture of thoracico-abdominal pleura in more helotrephid taxa) – especially in Helotrephidae.

CONCLUSIONS

- (1) The thoracico-abdominal sclerite is with a high probability of the abdominal origin. It is an anteriorly shifted rudiment of the first abdominal (dorsal) laterotergite.
- (2) The tribes Notonectini, Nychiini, subfamily Anisopinae, *Anisops* and *Buenoa* respectively (Notonectidae), Helotrephini, Limnotrephini (Helotrephidae), subfamily Trephotomasinae (Helotrephidae), and family Pleidae are well defined by the characters of the pterothoracic and basal abdominal regions of exoskeleton.
- (3) Fragmentary cladograms of the Notonectoidea and Pleoidea based only on the pleural pterothoracic and thoracico-abdominal architecture confirm the major features of Mahner's (1993) hierarchic classification, and show even the possible alternatives of problematic sections of Mahner's cladograms.
- (4) It is to presume that the complex of main characters of thoracico-abdominal pleura reflects the phylogenetic relationships, and it could be also used for the study of the phylogeny of Nepomorpha.

Acknowledgements

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Homologies of the reduviid genital capsule (Hemiptera: Heteroptera)¹

Carl W. SCHAEFER

Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269-3043 U. S. A.
e-mail: schaefer@uconnvm.uconn.edu

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Abstract. Dissection and study of three species of Reduviidae, of the subfamilies Ectrichodinae and Peiratinae, indicated strongly that the genital capsule (= pygophore) of the male cimicomorphan is homologous with that of male pentatomomorphans and aradomorphans. The capsule is almost certainly the modified ninth sternum, all or most of the ninth tergum having been lost. The capsules studied lack certain structures (transverse ridge, median projection) found in the other groups; and the presence of another structure (the cuplike sclerite) is uncertain. Nevertheless, these differences do not refute the hypothesis that the reduviid genital capsule is homologous with (has the same origin as) that of the Pentatomomorpha and Aradomorpha.

Morphology, genital capsule, pygophore, Heteroptera, Aradomorpha, Cimicomorpha, Pentatomomorpha, Reduviidae

INTRODUCTION

The genital capsule (= pygophore, etc.) of the male heteropteran contains the structures which introduce sperm into the female (aedeagus) and which aid that introduction (parameres, basal plate apparatus). Some years ago I studied the genital capsule of the heteropteran group Trichophora, and discussed its origins and development (Schaefer 1977).

The Trichophora (superfamilies Lygaeoidea, Coreoidea, Pyrrhocoroidea, and Pentatomoidea) plus Aradoidea compose the infraorder Pentatomomorpha; with the recent removal of Aradoidea to a separate heteropteran infraorder, Aradomorpha (Sweet 1996; but see Henry 1997), Trichophora (a name of no nomenclatorial validity) now includes the same heteropterans as Pentatomomorpha.

More detailed studies after my 1977 one, on several groups within the Pentatomomorpha, confirmed the ideas I presented in 1977 (see Schaefer 1978–1993, Schaefer et al. 1988, 1989; these ideas are confirmed also in unpublished work on Pyrrhocoroidea and Aradomorpha). Yet the generality of those ideas should be tested by looking at the genital capsules of heteropterans in other infraorders. I do this here, in a preliminary examination of the genital capsules of several reduviids (infraorder Cimicomorpha, family Reduviidae).

The Reduviidae is a very large and very diverse family (some 6000 species in about 25 subfamilies [Maldonado Capriles 1990]). I have studied the genital capsules of three species (two genera) in two subfamilies. My sample is far too small to draw conclusions either generally about the family, or particularly about phylogenetic relationships within the family.

My interest in this study has been more restrained. I wanted to see if the general structure of the reduviid genital capsule is the same as that of the capsules of pentatomomorphans; that is, to see if the capsules of these two groups are homologous. Also, I wanted to see if there was enough

¹This paper is dedicated with affection, respect, and in lieu of some single-malt liquor, to Prof. Dr. Pavel Štys. Like Mr. Chaucer's Clerk of Oxenford, "Gladly wolde he leme, and gladly teche."

difference among the genital capsules of Reduviidae that they might prove useful in working out phylogenetic relationships; for working out these relationships is necessary if an acceptable higher classification is to be developed. To this end I chose representatives of two subfamilies and also of a single genus to judge the degree of difference one might expect to find in Reduviidae.

If indeed the genital capsule of Reduviidae, and its parts, can be homologized with those of the Pentatomomorpha, then it makes more likely that the heteropteran capsule had a common (single) origin. It also makes it easier to compare capsules from different groups, and thus to establish phylogenetic relationships among these groups. And if these capsules vary among reduviid groups (tribes, subfamilies), and if the variation is not overwhelmingly great, then it becomes possible to analyze the variation to arrive at intrafamilial relationships – as has been done with some success in Pentatomomorpha.

The genital capsule may be thought of as a very short, rather stout tube; one end opens anteriorly (internally, into the body), the other end opens posteriorly (externally); through the external opening emerge the aedeagus and the proctiger. The anterior opening is usually a simple ring, and it may be displaced more or less dorsally. The posterior opening is more complex. I have argued (1977) that this opening, primitively posterior, has often (in various heteropteran lineages) become dorsal. This dorsalization renders *anterior* and *posterior* structures associated with the external opening which were ventral and dorsal when the opening was posterior. I use the morphologically correct terms “ventral” and “dorsal” even when (in the case of capsules with dorsal openings) the structure in question are anatomically (geographically) posterior and anterior, respectively.

Among such structures is the rim which surrounds the external opening. This rim is usually folded in, either perpendicular to itself (or to the capsule's surface) or wholly infolded and applied to the inner surface of the capsule. The rim is continuous; however, I distinguish dorsal, lateral, and ventral rims, because each of these is modified differently; dorsal and lateral rims are folded in perpendicular to their walls (if folded in at all); and the ventral rim is folded in more deeply, often becoming attached to the inner ventral wall (or the floor) of the capsule. The end of the infolded ventral rim may be thickened, as a *transverse ridge*; this occurs in some Pentatomomorpha (Schaefer 1977) but not in the few aradomorphans I have seen (unpublished).

Supported by the transverse ridge in many pentatomomorphans and aradomorphans is a median *cuplike sclerite* which itself supports a *median projection*; these at time protrude from the capsule's external opening, and together they probably support and guide the aedeagus. One or the other (or both) of these may be lost, and sometimes they are fused more or less indistinguishably.

The structures I describe (anatomy) are explained (morphology) within the framework of the ideas I developed from the genital capsules of Pentatomomorpha (Schaefer 1977). This may appear to be assuming the hypothesis I wish to test; but I point out that there is no competing hypothesis, and, more importantly, that I do not “force” the anatomy to conform to my morphological hypothesis. Always eager to eschew the confines of a hypothesis (even mine), I have scrutinized these genital capsules for features that would *not* fit the hypothesis.

METHODS

The reduviids were softened in hot water and their genital capsules removed with fine pins. The capsules were examined then and, for further study, were treated with hot KOH to remove soft tissue. In some cases the capsules' contents (aedeagus, basal plate apparatus, parameres) were removed.

Species examined: *Ectomocoris quadriguttatus*, *Ectomocoris ochropterus* (Peiristinae), *Haematorrhophus nigrovoluceus* (Ectrichodinae).

RESULTS

Peiratinae

Ectomocoris quadriguttatus (Fabricius, 1781) and *E. ochropterus* Stål, 1866

Eighth segment. Membranous dorsally (eighth tergum, 8T); well sclerotized ventrally and laterally (lateral sclerotization a continuation of the ventral) (eighth sternum, 8S); anterior border of 8S incised medially, anterior rim itself infolded slightly and forming supporting ridge; posterior border of 8S with long medial spinose projection, this fitting into a shallow groove on ventral surface of genital capsule; 8T with pair small sclerotized spiracles, these apparently functional (tracheae attached).

Genital capsule (ninth sternum). External opening dorso-posterior; internal opening dorso-anterior; the two openings confluent, separated only by tenth segment (proctiger) and its connection to base of aedeagus. Therefore no dorsal rim. Ventral surface of capsule dark posteriorly (posterior two-thirds), pale anteriorly (where covered by 8S), pale area continued posteriorly as shallow median groove for projection of 8S. Dorsal and lateral rims: See Note, below. No lateral rim apodeme. Ventral rim also turned in perpendicular to ventral surface, to a greater extent than dorsal and lateral rims; inturned region then infolded, infolding applied closely to inner surface of inturned region and, more deeply, fused with inner surface of capsule (=capsule's floor); inturned region well sclerotized, especially posteriorly (here confluent with and of same texture as ventral surface of capsule); infolding lightly sclerotized; inturned region ending abruptly at each lateral rim; inturned region clearly double-layered (ventral rim plus infolding) and, although thick, without space between layers (seen via transverse cut across inturned region). Without transverse ridge. Parameres articulating to infolding at juncture of ventral and each lateral rim. Ventral rim medially with large, scimitar-shaped, heavily sclerotized, asymmetrical projection (symmetrical in *E. ochropterus*) extending posteriorly between parameres (concealed by them when they at rest); projection solid (no space discernible within in optical section), but composed of ventral rim plus ventral rim infolding; thus an extension of the broad, well sclerotized, inturned region. No cuplike sclerite or median projection. Basal plate apparatus stout, well sclerotized; suspensory apodemes poorly defined, apparently joining inner wall capsule near (but internal to) region where parameres arise.

NOTE. The internal and external openings of the capsules of these *Ectomocoris* spp. have become a single opening, by the loss of the capsule's dorsal surface (and rim) which usually separates these two openings. As a result, there is no dorsal rim of the external opening, and the *ventral* rim of the *internal* opening, displaced somewhat dorsally, takes over this role. The lateral rims of the external opening are confluent with the lateral rims of the internal opening. These lateral rims are turned in perpendicularly, and, where they meet the dorsal rim (of internal opening), arises a small dorsally projecting apodeme; otherwise the dorsal and the lateral rims meet smoothly.

Tenth segment (proctiger). Lightly sclerotized dorsally, membranous ventrally; without ornamentation or thickenings; joined via membrane to base of aedeagus, and via lightly sclerotized membrane to juncture of lateral and ventral rims (where paramere articulated).

Ectrichodiinae

Haematorrhophus nigroviolaceus (Reuter, 1881)

Eighth segment. Membranous dorsally, well sclerotized ventrally and laterally; anterior border of sternum entire, infolded as a ridge, this with small medial posteriorly projecting apodeme; internal to ridge, on either side, narrowly ovoid region of clear cuticle [Note: this "window" resembles those in the same place in some Pyrrhocoridae (Schaefer unpubl.)]; each side of anterior border of sternum

ending in small ventrally projecting apodeme, posterior border of sternum entire, with small medial ridge, each side of posterior border ending dorsally in small medially projecting apodeme, no spiracles or spiracular remnants

Genital capsule External opening dorsal, slightly posterior, internal opening anterior, slightly dorsal. Dorsal surface membranous, except for narrow sclerotized band at dorsal rim, laterally, just posterior to band, at juncture of dorsal and each lateral rim, a very small irregular sclerite in membrane, sclerite loosely attached to dorsal rim, between proctiger and dorsal rim, laterally, embedded in membrane, pair of more heavily sclerotized V-shaped structures. Dorsal and lateral rims not turned in. No lateral rim apodemes. Parameres shallowly articulated at juncture of ventral and each lateral rim. Ventral surface dark, heavily sclerotized posteriorly (where exposed), paler, more lightly sclerotized anteriorly (where covered by 8S), anterior region at lower level than posterior, so latter rising suddenly as low "plateau". Ventral rim infolding complex: infolded perpendicular to surface, this perpendicular infolding bearing medially a sharp, laterally flattened, symmetrical, well sclerotized tooth (this flanked by long setae), infolding then continuing internally, becoming fused with floor of capsule, broad (perpendicular) region of infolding continuing laterally to lateral rim, at this point becoming internal for short way, supporting paramere, perpendicular region of infolding clearly double-layered (optical section). No transverse ridge. Pair of broad, thin, flaplike, lightly sclerotized structures arising laterally from near (but internal to) juncture of ventral and lateral rims, flaps joined on midline (cuplike sclerite?) and joined via membrane to perpendicularly infolded region of ventral rim. No median projection.

Tenth segment (proctiger) Lightly sclerotized posteroventrally, membranous anteroventrally and dorsally, without ornamentation.

DISCUSSION

The structure of the genital capsule in these three species of Reduviidae (representing two subfamilies) is very similar to that of the pentatomomorph capsule, the capsules are alike in overall structure, and in detail. There are some differences, but these are insufficient to disprove the hypothesis that the capsules of these two groups are fundamentally alike and therefore are likely to have had the same origin. The capsules are homologous.

I have two bases for this statement. First, the fact that all these capsules are so very much alike. And second, because the relationships of the intersegmental membranes are in these reduviids as they are in the Pentatomomorpha. Much of my argument for the origin of the pentatomomorph capsule was based on the relationships of these membranes with the sclerites to which originally (primitively) and now they have been and are attached (Schaefer 1977). I shall discuss the capsule and the membranes separately.

The genital capsule

Ninth tergum (9T) I found no clear evidence of 9T in these reduviids. This region of the capsule is often membranous (probably for flexibility of aedeagus and proctiger) both here and in many pentatomomorphans, so the lack of 9T remnants or other evidence is not unexpected.

In the *Ectomocoris* spp. 9T may be represented by the lightly sclerotized membrane which joins the proctiger laterally to the juncture of the lateral and ventral rims. If this is 9T, the proctiger must somehow have become incorporated into 9T (not perhaps an impossibility) in order to provide some support for the proctiger. The V-shaped sclerites in the membrane between the proctiger and the dorsal rim may be remnants of 9T in *Haematorrhophilus nigroviolaceus*. However, the sclerotized band with which these sclerites are associated probably is not, as its paleness and texture suggest it is a secondary sclerotization of part of the membrane. In all these reduviids, these sclero-

tized regions resemble what Davis (1966) calls in *Triatoma protracta* (Uhler, 1894) the "9T" ("ninth tergum"); but here too, this band may be a secondary sclerotization. Of course, in these reduviids, and in pentatomomorphans as well, the membrane itself is probably the desclerotized 9T.

Openings. If my scenario for the origin of the genital capsule is correct, the two openings (internal, external) were originally directly anterior and posterior; dorsalization, if it comes at all, comes later. The openings in the three reduviids I studied are all dorsal or partially dorsal: an advanced condition (if my hypothesis is correct). Indeed, in *Ectomocoris* spp. the two openings have each been so dorsalized as to meet and become confluent. This occurs also in some Alydidae (Schaefer 1980, Schaefer et al. 1989), and occurs commonly in Aradidae (Schaefer unpubl.).

Rims. The dorsal and lateral rims of *Haematorrhophus nigroviolaceus* are not turned in (bent over) at all; in pentatomomorphans, and in the *Ectomocoris* spp., these rims are turned in at least perpendicular to the walls of which they are the edges or margins. In none of the reduviids does the lateral rim bear a medially projecting apodeme; this occurs in nearly all pentatomomorphans, and is often well sclerotized and sometimes complex. However, in pentatomomorphans this apodeme forms part of the support for the paramere. In Reduviidae, the paramere is more external (less deeply inserted into the capsule), and such support as a lateral rim apodeme might provide is here unnecessary.

The infolding of the ventral rim, a common feature of the trichophoran genital capsule, occurs also in that of the reduviid. Indeed, Davis (1966) had already described this infolding (although somewhat ambiguously), and illustrated it (not at all ambiguously), in the capsule of *Triatoma protracta* (Davis 1966, fig. 7). This infolding doubtless serves at least two purposes: It strengthens the capsule itself (especially the more stressed posterior portion of the capsule) for the rigors of intromission and (an exaction) it has perhaps allowed the elaboration of other structures; I have suggested (1977: 295, 297) that the transverse ridge and perhaps the cuplike sclerite originated from the leading edge of the ventral rim infolding.

Of greater importance is the fact that if the genital capsule consists, as I believe, largely of the ninth sternum (and not of the entire ninth segment), and if – as I also believe – the genital capsule arose as a result of the internalization of the aedeagus, then the ventral rim of the genital capsule *must* be infolded (Schaefer 1977, especially fig. 12). And in these reduviids, it is.

In the pentatomomorphans capsule the leading edge of the ventral rim's infolding is sometimes (not always) thickened, as a transverse ridge. I have not found this structure in these reduviids (or in aradids).

Cuplike sclerite and median projection. These structures are probably lacking in the reduviids I studied. The thin, lightly sclerotized flaps arising at the level of the parameres' articulation (but internal thereto) in *Haematorrhophus nigroviolaceus* may be the cuplike sclerite. But they do not arise medially (from the capsule's floor) and, in shape and lightness of sclerotization, they do not resemble the cuplike sclerites I have seen in Pentatomomorpha (where, however, these structures may be lost). I found nothing that might be the cuplike sclerite in the *Ectomocoris* spp. However, Davis (1966) figures a structure (SA, in his Fig. 1) in *Triatoma protracta* which, arising posteriorly from the capsule's floor and articulating with the basal plate apparatus, both serves the function of and is in the same position as, the cuplike sclerite of Pentatomomorpha. Again, in some phymatines, Davis (1957) describes a structure which he identified with Singh Pruthi's (1925) "inferior process"; its position suggests it too may be the cuplike sclerite. Despite these possibilities, however, the presence of the cuplike sclerite (and of the median projection) in Reduviidae so far remains moot.

However, the presence of these structures is not a necessary part of the argument that the reduviid genital capsule is homologous with the pentatomomorphans one, if my explanation for their origin is correct (Schaefer 1977).

The posterior intersegmental membranes

The membranes uniting the seventh and eighth segments, and the eighth segment with the genital capsule, in the three reduviids I studied, are very much like those I described for pentatomomorphans (Schaefer 1977). If the genital capsule is a modification of the ninth sternum, then the intersegmental membranes should reflect this homology; they do in Pentatomomorpha and, I believe, they do also in Reduviidae. One difference is the attachment of the seventh-eighth intersegmental membrane; this joins the eighth sternum's anterior ridge not terminally, but subterminally (as it does also in the pentatomomorphan lygaeid *Oncopeltus fasciatus* [Dallas 1852] [Schaefer 1977]); that is, the membrane joins the anatomically terminal border of the eighth sternum, not the morphologically internal one, which is the leading edge of the ridge (the ridge being the inturned rim of the eighth sternum). As a result, the ridge is not covered by membrane and is "free" for the attachment of muscles, a function for which it is adapted by thrusting somewhat internally and being well sclerotized. This difference between the trichophoran and the reduviid eighth sterna does not affect the argument that the genital capsule in both groups is a modified ninth sternum.

The relationships of the membranes uniting the eighth segment and the genital capsule closely resemble those I have described for the Trichophora (see Schaefer 1977: 293–294). Of particular importance is the distinction in both groups between the membrane which joins the eighth sternum to the capsule, and the membrane which joins the eighth tergum to the capsule. The fact that these membranes are distinct supported my argument in 1977 that the genital capsule is of ninth-sternal origin; and it supports now my argument that the reduviid genital capsule has the same origin. For if the genital capsule were simply the entire ninth segment, the membrane joining it with the eighth segment would have been simple and complete. That this membrane is neither simple nor complete, suggests that either one of the two joined structures (or both) is (or are) considerably modified. The eighth segment is a simple ring, its dorsal and ventral regions demarcated by the spiracle (sometimes absent, but present often enough, in trichophorans and reduviids, to make assessment of eighth tergum and sternum easy). The actual arrangement of the membranes supports the idea that it is the ninth segment which is modified, and that in fact the ninth sternum has grown dorsally, to obliterate most of the ninth tergum and to form the genital capsule. The eighth-ninth intersegmental membrane is not wholly ventral, but extends dorsally to the level of the spiracle – as one might expect if the primitive ninth sternum had grown dorsally, carrying with it the membrane which joins it with the eighth sternum. Ending also at the level of the spiracle is a more dorsal membrane, which might be the eighth-ninth intertergal membrane, although this is uncertain. But none of the possible origins of this membrane (see Schaefer 1977: 298–299) vitiates the argument from the intersegmental membrane, that the genital capsule is a modified ninth sternum, in both the Pentatomomorpha and the Reduviidae.

Again, a membrane joins the tenth sternum (10S, proctiger) and the base of the aedeagus, as it does also in the Pentatomomorpha and as it should if the base of the aedeagus was carried in by the infolding of 9S (Schaefer 1977: 295). Here too, the evidence from this membrane supports the likelihood that the reduviid genital capsule has originated as has that of the Pentatomomorpha (and Aradomorpha, although I have not examined the relationships of the latter's membranes).

Parameres

Although not part of the genital capsule as I have studied it, the parameres of Reduviidae differ in an important way from those of the Pentatomomorpha (and many other heteropterans). In Reduviidae, the parameres lie almost entirely outside the genital capsule; in some reduviids (e. g., *Ectomocoris* spp.), they appear as posterior extensions of the capsule, an appearance heightened by their broad shape. Nevertheless, the parameres are articulated in Reduviidae in about the same position as they are in Pentatomomorpha: within the capsule (but more superficially) where the inner ventral

surface meets the inner lateral surface; projecting from the capsule directly from this point, the parameres in reduviids and other bugs are braced externally by the juncture of the lateral and ventral rims. But in Reduviidae, perhaps because the insertion of the paramere is shallow, no lateral rim apodeme has developed to provide additional bracing.

Arising more superficially, and thus lying lateral to the capsule rather than thrusting out from it, the parameres of some reduviids resemble the "hypopygidial appendages" of some Podopinae (Pentatomidae) (Schaefer 1981b, 1983) and of some other pentatomids (see Schaefer 1981b). The parameres of the two *Ectomocoris* species I dissected resemble even more closely the hypopygidial processes of such podopines as *Amaurochrous cinclipes* (Say, 1828); these parameres are broad, thickened, and double-layered (have a space within them, as shown by cross-sectioning). There is no phylogenetic significance in their similarity, but the resemblance is close, and of interest.

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The ovary structure and oogenesis in *Hydrometra stagnorum* (Heteroptera: Hydrometridae)

Bożena SIMICZYJEW

Department of General Zoology, Zoological Institute, Wrocław University, PL-50-335 Wrocław, Poland

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Abstract. The ovaries of *Hydrometra stagnorum* (Linnaeus, 1758) are of the telotrophic-meroistic type. Each of them is composed of seven ovarioles with apical terminal filaments, joining together into a suspensory ligament. Each ovariole consists of an anterior trophic chamber (tropharium), a posterior vitellarium and an ovariole pedicel which connects the ovarian tube with the lateral oviduct. The tropharium houses numerous individual trophocytes located around the acellular trophic core. The basal part of tropharium is filled with somatic prefollicular cells and young, early previtellogenic meiotic oocytes. The vitellarium contains linearly arranged ovarian follicles. An individual follicle is built of an oocyte surrounded by follicular epithelium. The oocytes are connected to the trophic chamber by means of a trophic cord, filled with highly oriented microtubules. The oogenesis in the studied species has been subdivided into previtellogenesis, vitellogenesis and choriogenesis (egg shell formation).

Oogenesis, telotrophic ovaries, tropharium, oocytes, follicular cells

INTRODUCTION

Two basic types of insect ovaries are recognized: panoistic and meroistic (Brandt 1874). In the panoistic ovary all oogonia can become oocytes. In meroistic ovaries, incomplete divisions of oogonia result in clusters (clones) of interconnected germ cells. The cells within the clone differentiate into oocyte(s) and nurse cells (trophocytes). Meroistic ovaries are subdivided into polytrophic and telotrophic (Gross 1903). In the polytrophic ovary each oocyte is accompanied by a group of nurse cells, whereas in the telotrophic one all trophocytes are retained in the anterior part of the ovariole, forming a tropharium (trophic chamber). In this type of the ovary the oocytes are connected with the trophic chamber by means of elongated cytoplasmic tubes (trophic cords). Telotrophic ovaries are characteristic of Hemiptera, Raphidioptera, Megaloptera (Sialidae), Coleoptera (Polyphaga) and Ephemeroptera. Although first morphological studies on heteropteran ovaries were done by Gross (1901, 1903), the morphology, ultrastructure and development of the telotrophic ovaries in Hemiptera have been extensively investigated during the last 20 years (for review see Büning 1994, Simiczyjew et al. 1998). The ontogeny of ovaries during larval stages of *Pyrrhocoris apterus* on light microscope level was described by Seidel (1924). Ultrastructure of the heteropteran ovary was studied in *Rhodnius prolixus* (Huebner & Anderson 1972a, b, c, Lutz & Huebner 1981), *Gerris remigis* (Choi & Nagl 1976, 1977a, b), *Saldula saltatoria* (Bilinski et al. 1990), *Nepa cinerea* and *Aradus pictus* (Simiczyjew et al. 1996), *Cryptostemma* spp. (Štys et al. 1998), *Macrosaldula variabilis* (Simiczyjew et al. 1998). These studies revealed that, besides general similarities, the ovaries of representatives of various suborders differ in the organization of the trophic chamber and in the differentiation as well as diversification of the follicular epithelium. The present paper describes the ovary structure and oogenesis in *Hydrometra stagnorum*, which is a member of poorly investigated suborder Gerromorpha.

MATERIAL AND METHODS

Specimens of *Hydrometra stagnorum* (Linnaeus, 1758) were collected in Zakrzów near Wrocław (SW Poland).

Light and transmission electron microscopy

Dissected ovaries were fixed in 2.5% glutaraldehyde in 0.1 M phosphate buffer, pH 7.4, at room temperature. The specimens were then rinsed and postfixed in 1% osmium tetroxide in the same buffer. After dehydration in a graded series of ethanol and acetone, the material was embedded in Epon 812. Semithin sections were stained with 1% methylene blue in 1% borax and examined in an Olympus BHS microscope. Ultrathin sections were contrasted with uranyl acetate and lead citrate and examined in a Tesla BS 500 electron microscope at 60 kV.

Fluorescence microscopy

The ovaries were dissected and fixed for 40 minutes in 4% formaldehyde, freshly prepared from paraformaldehyde in PBS at room temperature. Then the material was rinsed several times in PBS and stained with rhodamine-labeled phalloidin (1 µg/ml in PBS, Sigma) during 20 minutes. Following rinsing in PBS the material was stained with DAPI (1 µg/ml, Sigma), rinsed in PBS and examined in an Olympus BHS fluorescence microscope equipped with appropriate filters. Photographs were taken on Fuji Neopan 400 film.

Scanning electron microscopy

Eggs of *Hydrometra stagnorum* were stored in 80% ethanol, dehydrated in a graded series of ethanol, dried using hexamethyl-disilizane (Serva), mounted on SEM stubs with double-sided tape, coated with carbon and gold, and examined with Stereoscan 180 (British Cambridge Instruments) at 15 kV.

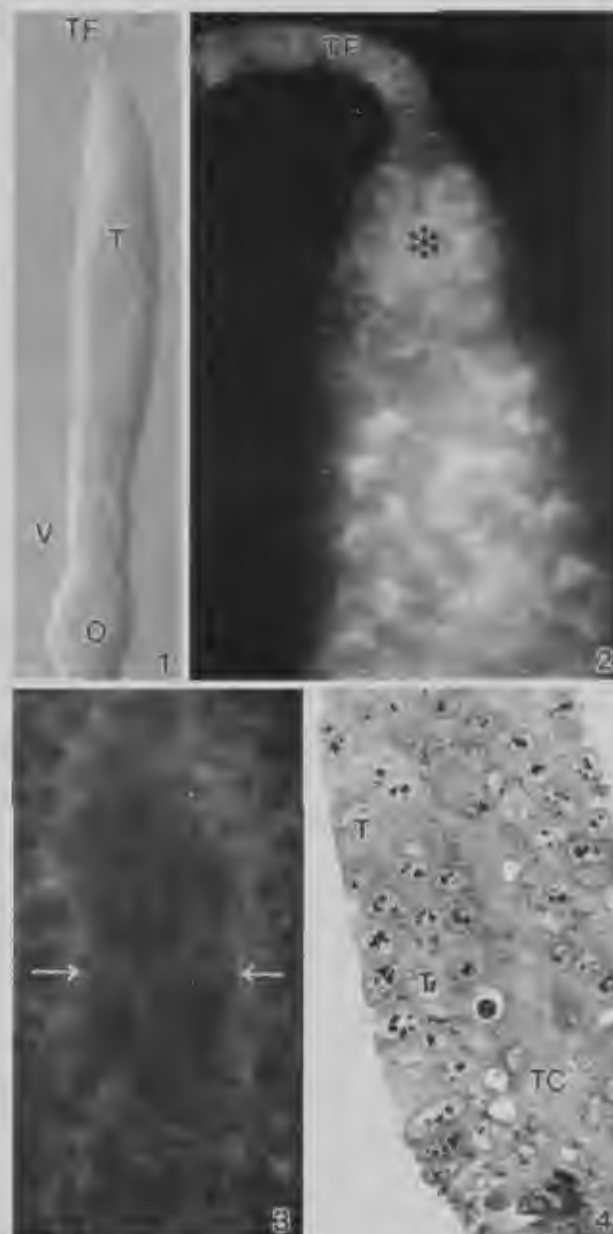
RESULTS

Gross morphology

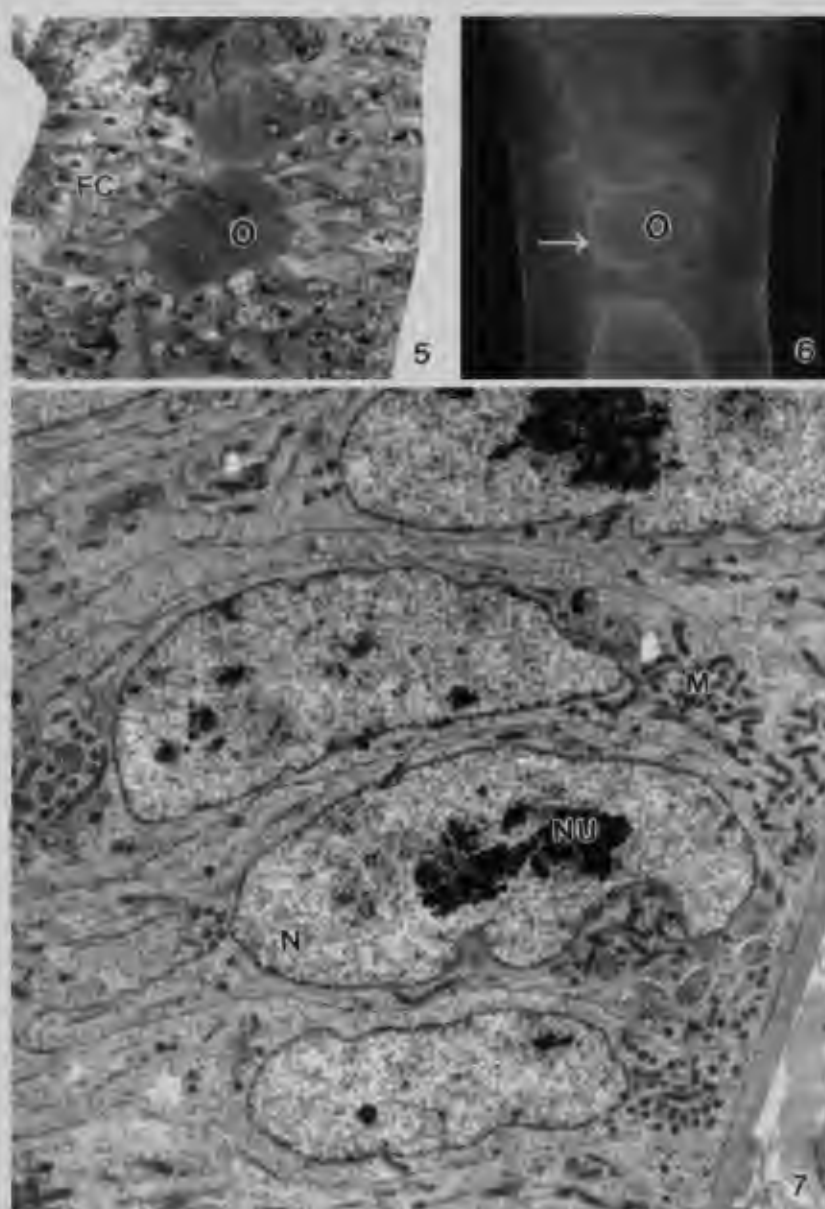
Each ovary of *Hydrometra stagnorum* consists of seven telotrophic ovarioles. An individual ovariole is differentiated into four regions: a terminal filament, a tropharium (trophic chamber), a vitellarium and an ovariole pedicel (Figs 1, 2, 5, 6). The terminal filaments join together to form a suspensory ligament. The trophic chamber is built of trophocytes (nurse cells), while the vitellarium contains linearly arranged ovarian follicles (oocytes surrounded by follicular epithelium – Figs 8–9). Each oocyte is connected with the trophic chamber by means of a nutritive cord (Figs 5–6), filled with masses of parallelly oriented microtubules. Lens-shaped cells of the terminal filament are oriented perpendicularly to the long axis of the ovariole (Fig. 2). The trophic chamber is spindle-shaped and houses numerous, individual trophocytes (Fig. 4). Some of the small trophocytes in the apical part of the trophic chamber divide mitotically, while some other possess regular nuclei with distinct nucleoli. More basally located trophocytes are bigger and surround the acellular central region termed trophic core (Fig. 4). The trophic core is filled with densely packed numerous microtubules and ribosomes. The microtubules are oriented parallelly to the long axis of the ovariole. Around the trophic core F-actin meshwork is observed (Fig. 3). The trophocytes are connected with the trophic core by thin processes (trophic processes) that are transparent in methylene blue-stained sections. In the basal part of the trophic chamber somatic, prefollicular cells and early previtellogenic oocytes occur (Figs 5, 7). Prefollicular cells are small, lens-shaped and oriented perpendicularly to the long axis of the ovariole (Figs 5, 7). The vitellarium contains a linear array of ovarian follicles at consecutive stages of oogenesis. The oogenesis in *Hydrometra stagnorum* has been subdivided into previtellogenesis, vitellogenesis and choriogenesis.

Previtellogenesis

At an early previtellogenic stage each oocyte is invested by several layers of identical follicular cells that at this stage do not form a regular epithelium (Fig. 5). At a mid- previtellogenic stage follicular cells form tight, mono-layer epithelium around the oocyte (Figs 8–9). Most of the volume of the follicle cell is occupied by the nucleus. In the cytoplasm mitochondria, free ribosomes and few dictyosomes are observed (Fig. 7). F-actin filaments in the basal part of follicular cells are



Figs 1-4. 1 - Phase-contrast micrograph of the ovariole. TF - terminal filament, T - tropharium, V - vitellarium, O - oocyte. $\times 45$. 2 - Apical part of the trophic chamber stained with rhodamine-phalloidin. A group of small trophocytes in the apical region is visible (asterisk). TF - terminal filament. $\times 200$. 3 - Middle part of the tropharium after rhodamine-phalloidin staining. Arrows indicate F-actin meshwork around the trophic core. $\times 180$. 4 - Longitudinal section of the trophic chamber. Epon, methylene blue. T - trophocytes, TC - trophic core. $\times 180$.



Figs 5-7. 5-6 - Basal part of the trophic chamber and the apical region of the vitellarium. 5 - Epon, methylene blue. $\times 320$. 6 - Rhodamine-phalloidin staining. O - oocyte, FC - follicular cells. Arrows indicate nutritive cord. $\times 180$. 7 - Electron micrograph of follicular cells surrounding early previtellogenic oocytes. N - nucleus, NU - nucleolus, M - mitochondria. $\times 9600$.

arranged in parallel bundles, perpendicular to the long axis of the ovariole (Fig. 10). During late previtellogenesis the oocyte is surrounded by tightly adjoining cylindrical follicular cells, cells which at this stage are binucleate. The nuclei are arranged one above the other along the apical-basal axis of the cell (not shown).

Vitellogenesis

During the vitellogenesis reserve materials are deposited in the ooplasm. At the beginning of this stage the uniform follicular epithelium differentiates into three morphologically distinct cell populations. The shape of follicular cells covering the lateral part of the oocyte changes to oval (Figs 12–13). Between the follicular cells spaces appear that make it possible for the yolk precursors to reach the oocyte (Fig. 12). In the cytoplasm, basally located F-actin filaments, previously forming parallel bundles, become irregular, lose their ordered arrangement, and the bundles cross each other (Fig. 11). The nuclei are situated next to one another, each containing a single nucleolus and chromatin accumulation (Figs 13, 14). The cells surrounding the anterior and posterior poles of the oocyte during vitellogenesis remain tightly packed. In advanced stages of vitellogenesis, the follicular cells become increasingly richer in dictyosomes, free ribosomes and rough endoplasmic reticulum. At the end of vitellogenesis they become flattened and the epithelium becomes compact again.

Choriogenesis

During this stage egg envelopes (egg shell) are deposited. All the layers of the egg shell in *Hydrometra stagnorum* are synthesized by the follicular epithelium (Figs 16–18). Precursors of egg envelope layers are stored in secretory vacuoles (Fig. 17). Then the latter are transported to the apical surface of follicular cells. Their contents is secreted to the space between the oocyte and follicular epithelium. There the material accumulates, fuses and forms layers on the surface of oocyte (not shown). Fully developed hydrometrid eggshell is built of three layers: vitelline membrane, endo- and exochorion. The vitelline membrane is thin and homogenous. The endochorion comprises a trabecular layer and a compact chorionic layer with many thin channels. The exochorion is complex and consists of air chambers, covered with a thin, porous chorionic layer (Fig. 16). The egg capsule comprises three specialized regions: the micropylar apparatus (Figs 15–16), the main body of the egg covered with ridges and the posterior pole with attachment disc (Figs 19–20) (for detailed description of the hydrometrid eggshell see Simiczyjew 1994).

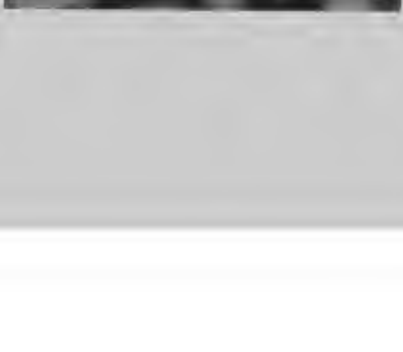
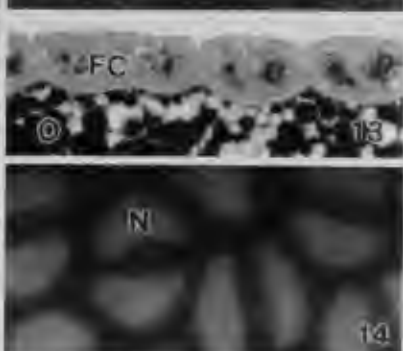
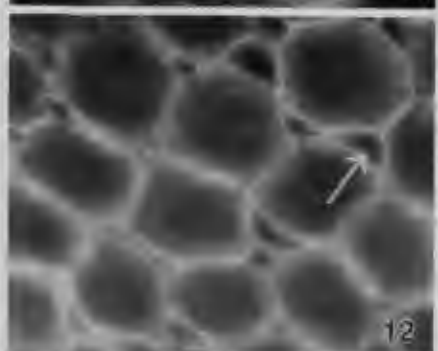
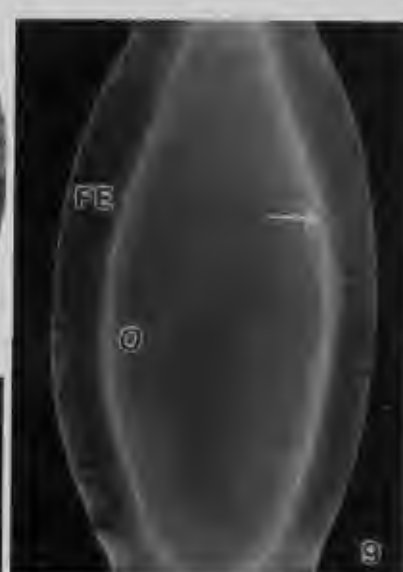
DISCUSSION

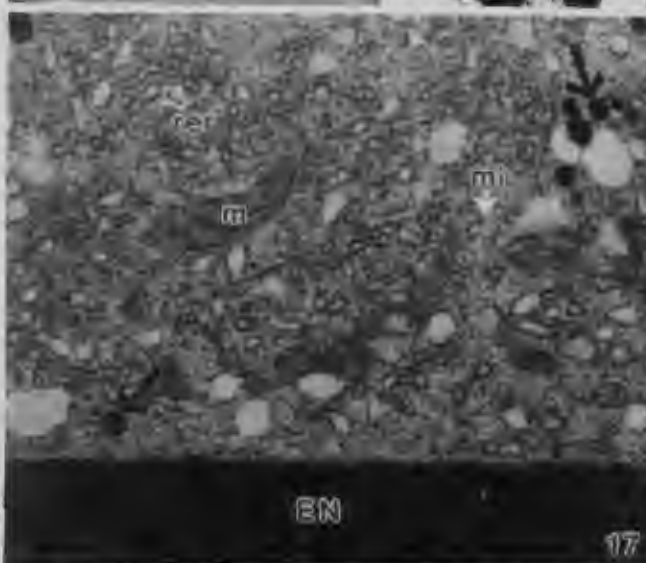
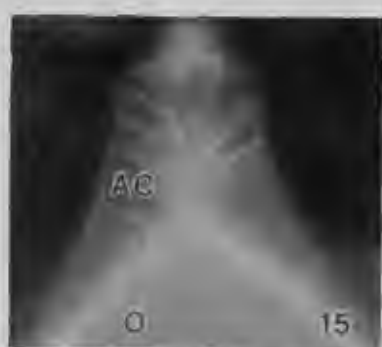
Recent morphological, ultrastructural and histochemical studies have revealed that the organization of the heteropterid trophic chambers is variable and differs between members of families and suborders. The tropharium of *Hydrometra stagnorum* consists of individual trophocytes. In other heteropterans of the infraorders: Gerromorpha (Choi & Nagl 1976, 1977a,b), Nepomorpha (Jawale & Ranade 1990, Simiczyjew et al. 1996) and Leptopodomorpha (Biliński et al. 1990) the organization of the trophic chamber is similar. In contrast, in more derived true bugs (Cimicomorpha: Reduviidae – Huebner & Anderson 1972c, Pentatomomorpha – Simiczyjew et al. 1996) the tropharia are composed of cytoplasmic lobes containing several trophocyte nuclei. The morphological gradient of the trophocyte nuclei within a trophic chamber in the species under study was also observed in other heteropterans (Huebner & Anderson 1972c, Choi & Nagl 1976, Huebner 1981, Simiczyjew et al. 1996). The tropharia of *Nepa cinerea* and *Aradus pictus* are morphologically diversified into 3 zones, in *Saltula saltatoria* and *Cryptostemma* spp into 2 zones (Biliński et al. 1990, Štys et al. 1998). In other heteropterans 3 or 4 zones can be distinguished (Sahai 1975, Bonhag & Wick 1953). In mirids no gradient exists and the trophic chamber is built of one type of nurse cells (Ma &

Ramaswamy 1987, Wightman 1973, Simiczjew et al. 1998). In *Hydrometra stagnorum* the apical zone of tropharium is occupied by mitotically active cells, although trophocyte divisions are rare. The apical region of mitotic divisions was also observed in *Oncopeltus fasciatus* (Wick & Honhag 1955), *Rhodnius prolixus* (Huebner & Anderson 1972c), *Dysdercus fasciatus* (Brunt 1971), *Gerris remigis* (Eschenberg & Dunlap 1966). No mitotically active trophocytes in the apical part of the trophic chamber were observed in members of Miridae (Wightman 1973, Ma & Ramaswamy 1987), Cimicidae (Davis 1956) and Dipsocoridae (Śtys et al. 1998). The analysis of the heteropteran tropharia and outgroup comparison (non-heteropteran Hemiptera: Książkiewicz-Kaprańska 1985, Szklarzewicz 1996, 1998) indicates that the individuality of the trophocytes and the absence of apical mitotic zone are ancestral characters in Heteroptera (Simiczjew et al. 1998). The well developed trophic core and trophic cords filled with numerous parallelly oriented microtubules in the studied species are shared by all the studied heteropterans (Lutz & Huebner 1981, Stebbings & Hunt 1982, 1983, Stebbings 1986, Büning 1994). The microtubules are engaged in the transport of various macromolecules (rRNA, mRNA) and organelles from the trophic chamber to the oocytes (MacGregor & Stebbings 1970, Gutzeit 1986, Anastasi et al. 1990, Münz & Dittmann 1987, Dittmann et al. 1984, 1987, 1990). In *Notonecta glauca* and *Dysdercus fasciatus* mitochondria are abundant in nutritive cords, while in *Corixa punctata* they are excluded from transport via microtubules (Hyams & Stebbings 1979, Stebbings 1988, Stebbings & Hunt 1987). In the trophic core and nutritive cords of the species under study only microtubules and ribosomes were observed. F-actin meshwork around the trophic core in *Hydrometra stagnorum* has been also found in other heteropterans (Huebner & Gutzeit 1986, Simiczjew et al. 1996, Śtys et al. 1998) and it is regarded as a component of the transport system between trophocytes and oocytes (Gutzeit 1986).

During the oogenesis follicular cells of *Hydrometra stagnorum* were found to undergo a series of changes in the morphology and ultrastructure, from cylindrical in the early previtellogenesis, through oval at the beginning of the vitellogenesis, flattened at the end of yolk formation stage. In the late previtellogenesis follicular cells in the studied species become binucleated. Binucleated follicular cells are found in other heteropterans (Huebner & Anderson 1972a) and mallophagans (Biliński & Jankowska 1987)). It has been suggested that they develop from mononuclear cells as a result of an amitotic division (Büning 1994). The development of spaces between the follicular cells during the vitellogenesis, termed patency, is hormonally regulated (Huebner & Anderson 1972a, Davey & Huebner 1974, Abu-Hakima & Davey 1977). It has been documented now that the cytoskeleton is responsible for the changes in the shape of follicular cells (Huebner 1976, Gutzeit 1990, Zhang & Kunkel 1992). The role of microtubules and microfilaments in the change of shape of follicular cells was studied in *Rhodnius prolixus* by Abu-Hakima & Davey (1977) and Watson & Huebner (1986). These studies revealed that the beginning of patency was correlated with reorganization of the microtubules in the follicular cells. In the previtellogenesis, in the follicular cells, forming a columnar epithelium, bundles of microtubules are arranged regularly, while in the advanced vitellogenesis their arrangement is random. Microfilaments in patent cells form distinct bundles, while columnar cells show no presence of microfilament bundles. The use of

Figs 8–14. 8 – Light micrograph of the ovarian follicle at the mid previtellogenic stage. FE – follicular epithelium, O – oocyte, n – oocyte nucleus. ×90. 9 – Previtellogenic ovarian follicle after rhodamine-phalloidin staining. Arrow indicates F-actin filaments in the cortical ooplasm. FE – follicular epithelium, O – oocyte. ×110. 10 – Follicular cells in previtellogenesis after rhodamine-phalloidin staining. Bundles of microfilaments are oriented parallelly (arrow). ×125. 11 – Follicular cells in vitellogenesis after rhodamine-phalloidin staining. Bundles of microfilaments cross each other (arrow). ×250. 12 – Follicular epithelium after rhodamine-phalloidin staining. Spaces between cells are visible (arrow). ×260. 13 – Follicular epithelium and part of the ooplasm in vitellogenesis. FC – follicular cells, O – ooplasm. ×250. 14 – Follicular cells after DAPI staining. N – follicular cell nucleus. ×280.





rhodamine-phalloidin made it possible to demonstrate that in the follicular cells of *Hydrometra stagnorum* bundles of actin microfilaments were present also in the previtellogenic epithelium and they were arranged parallelly, whereas in the vitellogenesis they crossed each other. The described parallel, linear arrangement of microfilaments shows similarities to "stress fibres" (Gutzeit 1990). They are typically present in the basal region of well-spread cells. The changes in the organization could be connected with a correlation between the reduction of cell adhesion to the basement membrane (Gutzeit 1990).

In *H. stagnorum* the originally uniform group of follicular cells diversifies into three subpopulations. Each of them builds a different region of the egg capsule. Huebner & Anderson (1972a), studying fine structure of vitellogenic ovarian follicles in *Rhodnius prolixus*, found that the follicular epithelium of the anterior pole of the follicle was tight and high prismatic, while the remaining follicular cells became spherical thus leading to the patency of this portion of follicular epithelium. It was demonstrated that, the compact compartment of the follicular epithelium, produced the sculptured cap of the egg capsule, whereas the remaining follicle cells were engaged in the formation of smooth chorion. The division of originally uniform group of follicular cells into distinct subpopulations, building various regions of the egg capsule, was found also in members of other insect orders: a dipteran *Drosophila melanogaster* (Margaritis 1985), a silk moths (Regier et al. 1980), an mallophagan *Eomenacanthus stramineus* (Biliński & Jankowska 1987). The results of biochemical studies reveal that morphologically different groups of follicular cells produce different sets of proteins, which most probably determines a definite differentiation of the chorion surface (Regier et al. 1980, Mazur et al. 1980, Papanicolaou 1985). For example, formation of aeropylar crowns in *Antheraea polyphemus* is no doubt associated with the synthesis and secretion of proteins E which are characteristic of the aeromicropylar crown region (Mazur et al. 1980).

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Figs 15-20. 15 - Anterior pole of the developing egg capsule. Rhodamine-labeled phalloidin. AC - air chamber, O - oocyte. $\times 90$. 16 - Apical part of the developing micropylar apparatus. Epon, methylene blue. FC - follicular cells, AC - air chamber, CH - chorion. $\times 170$. 17 - Ultrastructure of the follicular cell in choriogenesis. Prechorion granules (arrows) are visible. EN - endochorion, rer - rough endoplasmic reticulum, mi - microtubule, m - mitochondrion. $\times 14\,000$. 18 - Light micrograph of the follicular epithelium (FC) during egg envelope (EN) formation. Epon, methylene blue. $\times 110$. 19 - Part of the posterior pole of the egg capsule. Stalk (S) of the attachment disc is visible. Ex - exochorion, FP - follicular cell print. $\times 1400$. 20 - Longitudinal section of the developing attachment disc (AD). S - stalk, FC - follicular cells. Epon, methylene blue. $\times 220$.

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The systematic position of the Pamphantinae with the description of two new tribes and a new species of *Cattarus* (Hemiptera: Lygaeoidea: Geocoridae)

James A. SLATER

Department Ecology & Evolutionary Biology, University of Connecticut, Storrs, CT 06269, U. S. A.

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Abstract. The tribe Pamphantini is returned to its original subfamily status from its position as a tribe of the Bledionotinae. The genus *Cattarus* Stål, 1858 is analyzed and considered as a new tribe, the Cattarini trib.n. in the Pamphantinae. The tribe Epipolopini trib.n. is erected in the subfamily Pamphantinae. The genus *Phaeax* Distant, 1893 stat. n. is reduced to a junior synonym of *Cattarus*. *Cattarus styxi* sp. n. is described from South America.

Phylogeny, mimicry, Bledionotinae, Geocorinae, Pamphantinae, Epipolopini, Cattarini, Heterostarinae

The recent discovery of several undescribed species of pamphantines from the canopy of the South American rain forests and the reinterpretation of higher group relationships in the Pentatomomorpha have stimulated me to return to an analysis begun many years ago of the systematic position of the pamphantines.

For many years I have been doubtful that the New World pamphantine lygaeoids belonged in the same subfamily as the southern European genus *Bledionotus* Reuter, 1878, where they were placed by Scudder (1963).

It is a great pleasure to dedicate this paper to Professor Pavel Štys, my long time friend and colleague, who has contributed so much to our knowledge of the higher classification of the Heteroptera.

Reuter (1878) established the subfamily Bledionotina for *Bledionotus systellonoides* Reuter, 1878 from Syria. Barber & Bruner (1933) established the subfamily Pamphantinae for the genus *Pamphantus* Stål, 1874 from the West Indies.

Scudder (1963) reviewed the history of the Bledionotinae and Pamphantinae. He concluded that the two taxa were closely related and combined them into a single subfamily, the Bledionotinae, while still recognizing the new world components as a separate tribe, the Pamphantini. Scudder's (1963) paper was important not only because of the reduction of the Pamphantinae to tribal status but because he demonstrated clearly that despite a spiracle position similar to that found in myodochine Rhyparochromidae the type of spermatheca found in most rhyparochromine lygaeids was not present in the Bledionotinae (sensu Scudder) (Figs 12, 13) and this removed them from placement in the Rhyparochrominae where China & Miller (1959) and Slater & Hurlbutt (1957) had suggested they might belong. Scudder (1963) also removed *Cattarus* from the Rhyparochrominae and placed it in the tribe Pamphantini. (Note the similarity of the sperm reservoirs and parameres (Figs 7, 8, 9, 11), Scudder (1963) also noted similarity in many ways to the Geocorinae.

Just a year prior to the appearance of Scudder's paper Woodward (1962) had studied the genus *Phaeax* Distant, 1893 which the latter had placed in the Largidae, and concluded that it belonged in the Rhyparochrominae as a "somewhat aberrant myodochine". Seidenstücker (1964) stated his

belief that *Bledionotus* was an ant mimetic myodochine, and removed a second Palearctic genus that had been placed in the Bledionotinae (*Bethylimorphus* Lindberg 1953) to the Oxycareninae. Sweet (1967) in his seminal study of the relationships of higher taxa within the Rhyparochrominae also studied *Phaeax* and concluded that it belonged in the Bledionotinae. Sweet (1967) was apparently the first worker to note the stridulatory apparatus on the head and forefemur of *Phaeax* species and to relate them closely to *Cattarus*.

Subsequently Slater (1981a, 1981b) and Brailovsky (1989) have described new taxa in the Pamphantini. Slater's (1981b) paper described a new genus from northern Queensland and stated that his 1981a paper had reviewed the taxonomic history of the group. This unfortunately was not the case, the statement having been based on an unfinished study treated here. Brailovsky's (1989) paper described the first pamphantines from the rain forest canopy and included a key to the Western Hemisphere genera.

Henry (1997) believed that the Bledionotinae, Geocorinae and Henestarinae formed a monophyletic group defined by "the reniform eyes, dorsal abdominal spiracles on segments two, three and four and the two dorsal abdominal sutures between terga 3-4 and 4-5 that curve strongly posteriorly from the lateral margins of the abdomen to the gland openings on the meson in the 'nymphs'". Henry (1997) raised the Geocorinae to family status (the Geocoridae) and recognized three subfamilies the Geocorinae, Bledionotinae and Henestarinae.

Henry (1997) did not discuss the systematic position of the bizarre stalk-eyed Neotropical bugs of the genus *Epipolops* Herrich-Schaeffer, 1850. Stål (1868) placed the genus in the Geocorida where it remained until Ashlock (1957) placed it in the Cyminae. Hamid (1975) stated his belief that *Epipolops* definitely did not belong in the Cyminae, but did not place it in the existing classification system. Brailovsky (1990) treated *Epipolops* in the Pamphantini, but did not give evidence for his action.

The species of *Epipolops* are so wildly apomorphic that it is understandable that they have been a perplexing taxon.

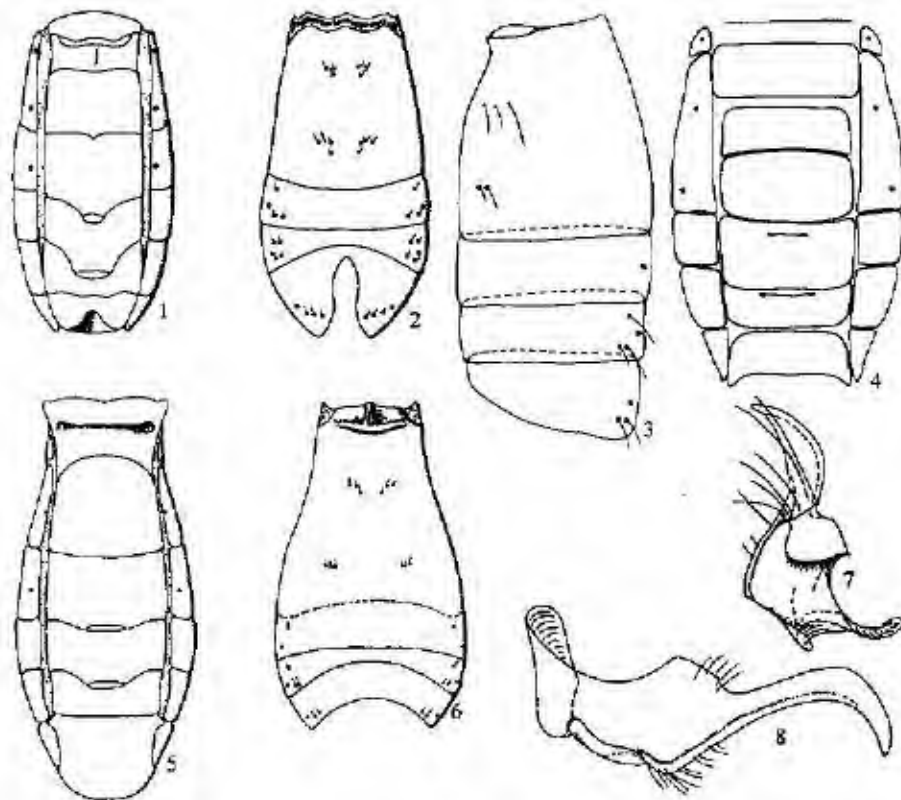
Sweet (in litt.) many years ago noted the similarity of species of *Epipolops* to the Pamphantini in the large punctures circled with cuticle, the fusion of connexiva two and three with the suture obliterated (Fig. 17) (synapomorphy), R and M veins not fused, the metacoxae nearly contiguous, the metasternum acute and the fusion and elimination of the sutures of the anterior abdominal sterna (Fig. 18). The sperm reservoir (Figs 19, 20) also agrees with the condition found in the pamphantines. As does and make "the" lower the simple elongate phallus (Fig. 19) and the paramere (Fig. 22). The spermatheca (Fig. 21) is more complex however and suggests that the tribal position advocated here is appropriate. *Epipolops* thus appears to be part of the expanded concept of the Geocoridae with close cladistic relationships to the pamphantines. I treat it here as a tribe within the Pamphantinae.

Scudder (1963) combined the Bledionotinae and Pamphantinae into a single subfamily because of the fused abdominal sterna 2, 3 and 4, the position of the abdominal spiracles (2-4 dorsal, 5-7 ventral), the straight suture between sterna 4 and 5, the presence of only 2 dorsal abdominal scent gland openings (between terga 4-5 and 5-6) and the caudal curving from the lateral margins to the meson of the abdominal sutures between these terga and especially the non-rhapharochromine nature of the spermatheca. His subsidiary characters, such as a tendency toward brachyptery, general appearance, reduction in membrane venation, relatively long claval commissure, only three rows of claval punctures, lack of a hamus in the hind wing, presence of long body hairs, and an ecarinate or weakly carinate pronotum are all features that occur over and over again in the Lygaeoidea and are of only secondary value at best in understanding relationships at tribal and subfamily levels. It is my belief that the Pamphantini and Bledionotini of Scudder (1963) are not sister taxa. I believe that Scudder (1963) was misled by the generally myrmecomorphic appearance of many of these species.

There are a number of important differences between these taxa that suggest convergence rather than close cladistic relationship. (A number of these differences were first brought to my attention by Dr Sweet).

While the fusion of the anterior abdominal segments is similar in the two taxa, the condition of these segments differ considerably in detail. The overall similarity seems to be due to convergence resulting from ant mimicry. These differences may be summarized as follows in a comparison of the two type genera, *Bledionotus* and *Pamphantus*:

Bledionotus-abdominal connexiva 3 and 4 fused and suture obliterated; 2 trichobothria present on segment 4; no trichobothria on segment 5 (Fig. 3); no intersegmental sutures visible on sterna 2-4; scent gland openings posterior to intersegmental sutures (Fig. 4); connexivum 7 in one piece (Fig. 4). Hind wing with R+M fusion; R joining marginal SC; hamus present; long prominent secondary veins present. Front wing with M present as a branch from R; medial fracture straight, short, stopping before divergence of M; punctures small, not areolate; SC indicated in membrane by a

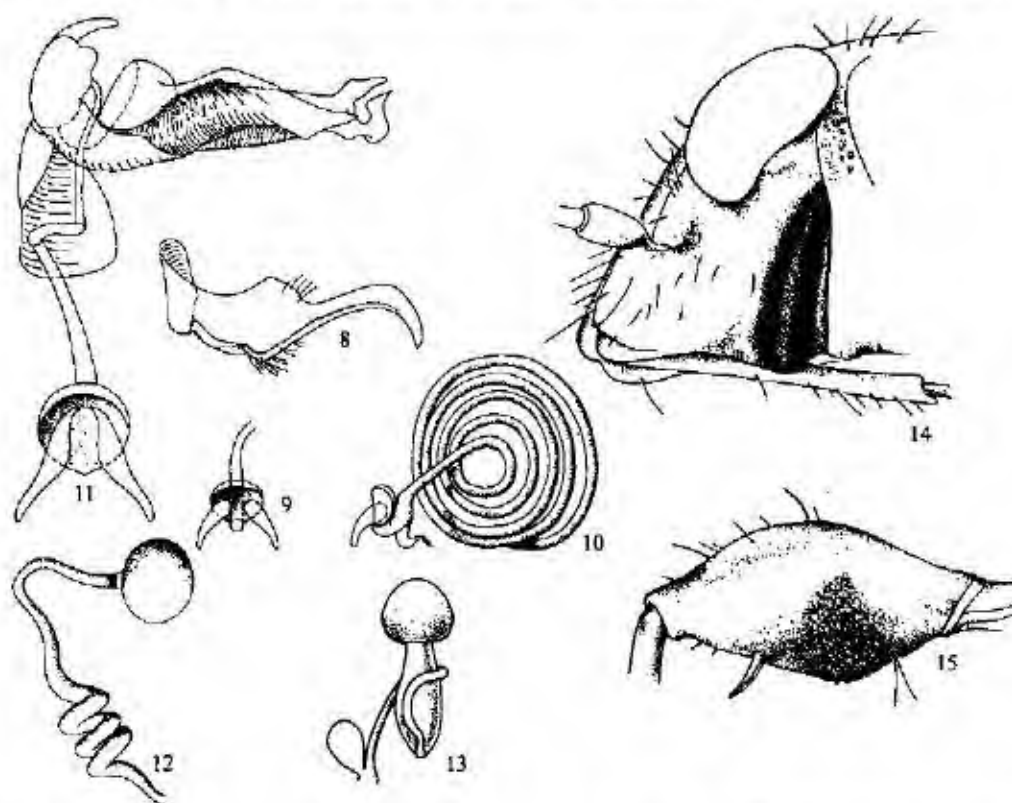


Figs 1-8. 1 - *Pamphantus elegantulus* Stål - abdomen dorsal view; 2 - abdomen ventral view; 3 - *Bledionotus systellanoideus* Reuter - female abdomen lateral view; 4 - female abdomen dorsal view; 5 - *Cattarus insignis* Stål - abdomen dorsal view; 6 - abdomen ventral view; 7 - *Pamphantus elegantulus* - paramere; 8 - *Cattarus insignis* - paramere.

concave vein (as in Oxycarenidae). Metacoxae widely separated (as in Oxycarenidae); metasternal spine process broad and truncate; femora slender, mutic; spurs present on hind coxae. Bucculae low but elongate; head surface hirsute including trichobothria-like hairs.

Pamphantus-abdominal connexiva 2 and 3 fused and suture obliterated; 4 trichobothria present on segment 4; 2 or 3 trichobothria on segment 5 (Fig. 2); sutures on segments 2-4 faintly visible in cleared specimens; scent gland openings conventionally located on intersegmental sutures (Fig. 1); connexivum 7 usually subdivided. Hind wing with R just touching M, not fused; R not joining SC; hamus absent; no secondary veins. Front wing with M absent; medial fracture long, sinuate, attaining posterior margin of corium; punctures large and arcolate. SC apparently absent in membrane. Metacoxae nearly contiguous. Metasternal spine pointed. Femora incrassate with a ventral spine (variable in Pamphantinae); no spine on hind coxae. Bucculae short, meeting behind labium; head without numerous hairs; eyes large, often reniform.

These differentiating features seem to preclude the position of the two taxa in the same subfamily. The habits are also suggestive of different evolutionary histories. Although relatively little is known of the biology of most species we do know that *Bledionotus* is a ground living insect



Figs 9-15. 9-10. *Pamphantus elegantulus* Stål. 9 - sperm reservoir, dorsal view; 10 - phallus with sperm reservoir in lateral view. 11 - *Cattarus insignis* Stål - phallus. 12 - *Pamphantus elegantulus* - spermatheca. 13 - *Bledionotus systellonotus* Reuter - spermatheca. 14-15 - *Cattarus insignis*. 14 - head, lateral view; 15 - fore femur.

whereas, at least the majority of, the pamphantines live on vegetation, some high in the forest canopy.

The condition of the head and forefemoral stridulatory apparatus in *Cattarus* (Figs 14, 15) is remarkably similar to that found in the Colobathristidae (which also have spiracles of segments 2, 3, 4 dorsal) but which do not have a lacinate ovipositor. Henry (1997) believed that differences in the condition of the ovipositor to have been over emphasized but I feel further analysis is required here.

No matter at what level the higher categories now included in the Lygaeoidea will ultimately be treated (separate families etc.) the present relationships of Scudder's inclusive Bledionotinae seem better expressed by elevating the Pamphantini to a separate subfamily the Pamphantinae thus returning them to the status originally proposed by Barber & Bruner (1933), but segregated into three tribes the Pamphantini, Cattarini, and Epipolopini.

All measurements are in millimeters. References to genera not included in the terminal list may be found in Slater (1964) and Slater & O'Donnell (1995).

Cattarini trib. n.

Type genus: *Cattarus* Stål, 1858: 41.

The recognition of *Cattarus* as a tribe separate from the nominate Pamphantini is based upon the following: abdominal spiracle two lateral or ventral (Fig. 5) rather than on the dorsal tergite; head with a large crescentic stridulitrum (Fig. 14) and tuberculate fore femoral plectron (Fig. 15); a proximal flange present on the spermatheca; three rather than four trichobothria on each side of abdominal segment 4 (Fig. 6); distinct lateral apodemes on tergum 8; a very complex phallus (Fig. 11) in contrast to the simple but very elongate and coiled condition (Fig. 10) of *Pamphantus*.

***Cattarus* Stål, 1858**

Cattarus Stål, 1858, 41

Phaeax Distant, 1893: 413 *syn. n.*

Type species: *Cattarus insignis* Stål 1858: 41 (monobasic).

Scudder (1963), described the genus in detail and illustrated the spermatheca. Scudder's description is excellent although some features appear to be specific to *C. insignis* rather than of generic significance.

The genus is remarkable because of the striking head-fore femoral stridulatory mechanism (the stridulitrum is illustrated but not commented on by Scudder (1963) and the plectron of *Phaeax* was illustrated although apparently not realized as part of a stridulatory apparatus by Woodward (1962). The position of the spiracle on abdominal segment two is unusual. Apparently it should be considered ventral morphologically although actually it is located in the membrane rather than on the sclerite. (The position of this spiracle is well illustrated in Woodward (1962)). Sweet (1967) agreed with Scudder's placement of *Cattarus* in the latter's inclusive Bledionotinae and noted the close relationship of *Phaeax* to *Cattarus*. He pointed out that *Phaeax* has a head stridulitrum.

Although due to import problems at the time this paper was written I was not able to examine the types of the two species of *Phaeax* in the Natural History Museum (London), Dr R. M. Baranowski (in litt.) has examined both types and has found no significant generic differences. He believes that neither of Distant's species is conspecific with any of the South American species from the forest canopy one of which is described in the present paper. There seems no doubt but that the two genera are synonymous and *Phaeax* is here formally placed as a junior synonym of *Cattarus*.

Cattarus stysi sp. n.

(Fig. 16)

DESCRIPTION. Coloration chiefly black, shading to dark brown. Head mesally, anterior pronotal lobe and scutellum black. Jugal and broad lateral area of head dull yellow. A narrow yellow stripe across anterior pronotal margin. Posterior pronotal lobe mesally broadly pale yellow, lateral two-thirds fuscous. Inner half of clavus and corium caudad of apex of clavus rich red-brown, outer one-half of clavus contrastingly yellow. A broad white transverse fascia across corium at level of distal one-half of claval commissure. Corium anterior to this fascia dark brown laterally, pale yellow mesally with a line of contrastingly dark punctures adjacent to claval suture. Membrane complexly variegated as follows: extreme basal area black, becoming yellow at level of middle of apical corial margins, a broad white crescent shaped transverse band across membrane beginning laterally just caudad of apex of corium, curving anteriorly between coria mesally, area immediately caudad of white band fumose with veins dull yellow. Fore and mid acetabulae laterally and posterior metapleural lobe white. Hind acetabulae yellow-brown, concolorous with trochanters and most of femora and fore and middle tibiae, hind tibiae contrastingly reddish-brown for most of length, becoming pale yellow-tan on distal ends. Antennal segment one pale yellowish-brown. Abdominal venter red-brown with strongly contrasting orange-yellow connexiva on segments 5-7 and anterior one-half of connexivum 4. Body and legs clothed with numerous elongate upright hairs, also with numerous declivent silvery hairs on transverse pronotal impression, head laterally and scutellum. Head and swollen calli area of anterior pronotal lobe nearly impunctate. Pronotum with a series of deep anastomosing punctures immediately behind smooth anterior margin. Posterior pronotal lobe and scutellum conspicuously punctate. Clavus with three rows of punctures. Body surface shining, except for pruinose clavus and a broad pruinose fascia on anterior one-half of dark corial color immediately behind white transverse fascia.

Head sloping downward anteriorly, first antennal segment almost attaining apex of tylus. Length head 0.94, width 1.52, interocular space 0.96. Anterior pronotal lobe swollen, strongly elevated above posterior lobe with width greater than that across humeral angles. Length anterior pronotal lobe 0.90, width 1.22, length posterior pronotal lobe 0.62, width 1.10. Scutellum small, somewhat elevated mesally. Length scutellum 0.56, width 0.62. Length claval commissure 0.62. Hemelytra strongly constricted mesally, narrowest at level of distal end of claval commissure. Membrane attaining middle of abdominal tergum 7. Midline distance apex clavus-apex corium 1.00. Midline distance apex corium-apex abdomen 1.82. Abdomen strongly constricted basally. Middle and hind femora enlarged. Fore femora incrassate, a sharp spine present on venter at distal one-third. Plectron an elevated group of short tubercles ventrally on proximal one-third of femora. Head stridulum elevated. Metathoracic scent gland auricle straight, evaporative area very large occupying entire anterior lobe of metapleuron. Labium extending at least to middle of mesosternum. Length labial segments I 0.46, II 0.50, III 0.40, IV 0.50. Antennae stout, segments three and four fusiform. Length antennal segments I 0.30, II 1.16, III 0.70, IV 0.80. Total body length 6.40.

TYPE MATERIAL. **Holotype** Male. BRAZIL: Minas Gerais Vicosa, Corrego de Paraíso (Mata do Prefeitúra) 10 III.1993 (T. J. Henry). In National Museum of Natural History (USNM), Washington, D.C. **Paratype** 1 female. Same data as holotype.

ETYMOLOGY. Named in honor of Dr. Pavel Štys my colleague and friend of many years for his many important contributions to our knowledge of the Heteroptera.

DIFFERENTIAL DIAGNOSIS. *C. stysi* sp. n. may be readily separated from *C. insignis* Stål, the only other described species, by being much more elongate, the length of the body being more than five times the width across the pronotal humeri, whereas in *C. insignis* the body length is less than 4 3/4 the



Fig. 16. *Calanus ovus* sp. n. - dorsal view.

humeral width. The claval color in *C. stysi* sp. n. is variegated with the inner half dark brown and the outer half yellow whereas in *C. insignis* the clavus is uniformly colored.

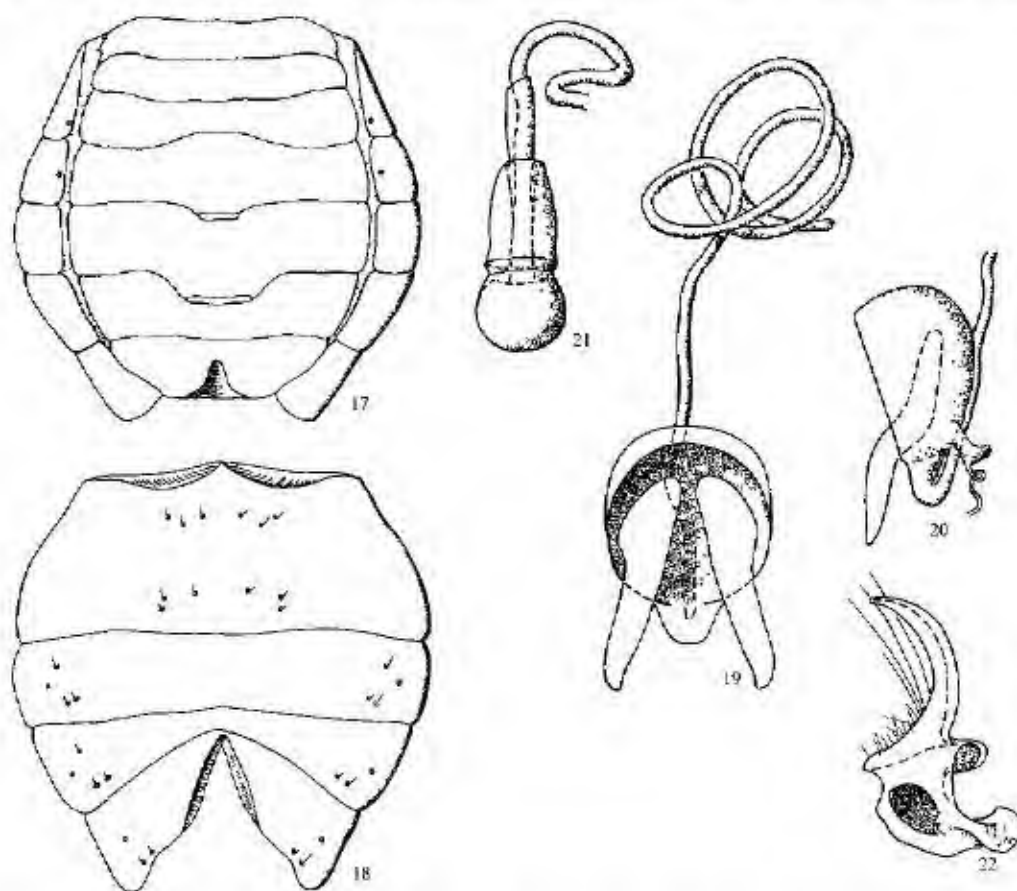
Henry (in litt.) noted that specimens in the field closely resembled wingless hymenopterans, possibly ponerine ants.

Several additional species of *Cattarus* and an undescribed genus occur in the South American rain forest canopy. These taxa will be described in a subsequent paper.

Epipolopini trib. n.

Type genus: *Epipolops* Herrich-Schaeffer, 1850: 191, 201.

Eyes somewhat reniform, placed upon elongate divergent stalks. Body broad and flattened. Pronotum with paired lateral (often lobate) projections. Claval commissure well developed, elongate.



Figs 17-22. 17-18 - *Epipolops meridionalis* Piran. 17 - abdomen dorsal view, 18 - abdomen ventral view. 19, 22 - *E. meridionalis*. 19 - phallus and sperm reservoir, dorsal view, 20 - sperm reservoir, lateral view, 21 - spermatheca, 22 - paramere.

Abdominal sterna 2–4 fused with sutures obliterated. Abdominal spiracles ventral on segment two, dorsal on segments three and four, ventral on segments 5–7. Sutures between abdominal terga 4–5 and 5–6 not strongly curving caudad from lateral margins to meson. Head lacking a stridulitrum. Punctures on dorsal body surface circled with cuticle. Metacoxae nearly contiguous.

ADDITIONAL COMMENT. Henry (1997) placed the Henestariinae as a subfamily of the Geocoridae. I have not studied this taxon and accept Henry's conclusions for the present.

Bledionotus does appear to be a member of the Geocoridae chiefly because of the spiracle position and the type of spermatheca (Fig. 13). However, the peculiar position of the abdominal scent glands (Fig. 4) and several features that are similar to those otherwise found only in the Oxycarenidae (of Henry 1997) suggests further study to be in order.

The subfamily Geocorinae itself is more complex than Henry's diagnosis might suggest. There is variability in the position of the anterior spiracle, the presence or absence of a claval commissure and in the degree of caudal curvature of the sutures between abdominal terga 4–5 and 5–6 in different genera.

The classification proposed here is as follows:

Geocoridae Stål, 1862

Geocorinae Stål, 1862

- Geocoris* Fallén, 1814
 - subg. *Eliatus* Linnavuori, 1972
 - subg. *Picocoris* Stål, 1872
- Geocoroides* Distant, 1913
- Germalus* Stål, 1862
- Hypogeocoris* Montandon, 1913
- Isthmocoris* McAtee, 1914
- Malloccoris* Stål, 1872
- Nesogermalus* Bergroth, 1916
- Ninyas* Distant, 1882
- Pseudogeocoris* Montandon, 1913
- Stenogeocoris* Montandon, 1913
- Stenophthalmicus* Costa, 1875
- Stylogeocoris* Montandon, 1913

Pamphantinae Barber et Bruner, 1933

- Pamphentini Barber et Bruner, 1933
 - Abpamphantus* Barber, 1954
 - Austropamphantus* Slater, 1981
 - Neopamphantus* Barber et Bruner, 1933
 - Pamphantus* Stål, 1874
 - Parapamphantus* Barber, 1954
 - Tropioparapamphantus* Brailovsky, 1989

Cettarini trib. n.

- Cattarus* Stål, 1858

Epipolopini trib. n.

- Epipolops* Herich-Schaeffer, 1850

Bledionotinae Reuter, 1878

- Bledionotus* Reuter, 1878

Henestariinae Douglas et Scott, 1865

- Coriantipus* Bergroth, 1912
- Engistus* Fieber, 1864
- Henestaris* Spinola, 1837

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I am much more than usually indebted to Dr Merrill H. Sweet (Texas A. & M. University, Texas) and Dr Abdul Hamid (Hamden, Connecticut) for allowing me to use data and sketches from work on this complex undertaken many years ago. Dr Thomas Henry (National Museum of Natural History (USNM), Washington D. C. made the study possible by sending me invaluable material that he had collected and from the rain forest canopy studies underway by the Smithsonian Institution. My deepest thanks are extended to Ms. Mary Jane Spring (University of Connecticut) for the dorsal view illustration of *Cattarus systi* sp.n. My appreciation is also extended to Dr R. M. Baranowski (University of Florida, Homestead Florida) for examining the type material of *Phaeax* in the Natural History Museum, London.

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Comparative morphology and taxonomic indications of the aedeagus in the genus *Aelia* (Heteroptera: Pentatomidae)

Brian W. STADDON & G. Abbas ABDOLLAHI*

School of Pure and Applied Biology, University of Wales, P. O. Box 915, Cardiff CF1 3TL, United Kingdom

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Abstract. The paper describes and compares the structure of the aedeagus in Pentatomidae representative of three species-groups in the genus *Aelia* Fabricius, 1803 and, for reasons of closeness, includes representatives of the genus *Neottiglossa* Kirby, 1837. The *Aelia acuminata*-group (as represented by *A. acuminata* Linnaeus, 1758) seems to bear a close relationship to *Neottiglossa*; the *Aelia rostrata* Rey, 1888-group is considered distinct, while the *Aelia virgata*-group is abundantly distinct from either the *Aelia acuminata* or *A. rostrata* groups. In the case of the *Aelia virgata*-group, the two species examined (*A. virgata* Klug, 1845, *A. albivittata* Fieber, 1868) are so different that they might seem to represent different genera. In the light of the data presented it is suggested that the classification of the Aeliini cannot be regarded as finally settled. It is evident that the character of the aedeagus is taxonomically useful in subdivision but at the same time remains unclear whether it tends to push widely apart species or groups that ought to remain together. We digress only to include a note on the spermatheca to the effect that the spermathecal dilatation in *Aelia albivittata*, uniquely so far as we are aware among Aeliini, is vestigial and presumably without function.

Morphology, genitalia, aedeagus, spermatheca, phylogeny, Heteroptera, Pentatomidae, *Aelia*, *Neottiglossa*

INTRODUCTION

The structure of the aedeagus and its bearing on the classification of the species presently comprising the pentatomid genus *Aelia* is the principal subject of the present paper. The paper also includes descriptions of the aedeagus in the genus *Neottiglossa* owing to its being placed together with *Aelia* in the tribe Aeliini (Wagner 1966).

The present subdivision of the genus *Aelia* into species-groups is due to Wagner (1960). The groups are separated by gross differences in size, shape, and appearance; in males they are separated by differences in the form of the upper border of the pygophore, by differences in the character of the parameres, and, as shown by Voegelé (1960, 1968) by differences in the character of the male genitalic superior processes. The latter occupy the male genital chamber alongside the parameres and are similarly paired; according to Dupuis (1959, 1970) they are phragmal in nature.

Wagner (1960), in a comprehensive study of the Palaearctic species of *Aelia*, described the copulatory process but otherwise provided little information on the structure of the aedeagus. However, descriptions of the aedeagus in several Aeliini, some more complete than others, have been provided by Voegelé (1960: *Aelia acuminata*, *A. cognata*, *A. germari*), Sisli (1964: *A. rostrata*), and McDonald (1966: *A. americana*, *Neottiglossa trilineata*). Here in seeking to confirm and extend previous work we provide some entirely new information on the structure of the aedeagus

*Present address: Sunn Pest Department, Plant Pests and Diseases Research Institute, P. O. Box 1454, Tehran, Iran

in species from Wagner's (1960) *Aelia virgata*-group. Our observations confirm the taxonomic value of the aedeagus in subdivision; at the same time they suggest that the classification of the Aeliini cannot be regarded as settled. We only digress to report what appears to be an unusual condition of the spermatheca in *Aelia albobittata*.

The initial work was undertaken by the junior author in Cardiff as a contribution to the sunn pest problem (*Aelia*, *Eurygaster* Laporte, 1832) in Iran (Abdollahi 1996). It was later extended and brought to its present form by the senior author who alone is responsible for the drawings and the interpretations contained herein.

TAXONOMIC BACKGROUND

The tribe has been treated by Wagner (1966).

Aeliini Stål, 1872

The members of this tribe are distinguished by having the body a yellowish-brown colour, the head somewhat pointed, the cheeks extending beyond and enclosing the tylus, the thorax with a prosternal sulcus, the scutellum large and with a distinct fold on each side. The species of *Aelia* and *Neottiglossa* are predominantly Palaearctic in distribution with some extension into the Nearctic and Oriental regions. They commonly occur on grasses (Gramineae), sometimes in large numbers; certain species of *Aelia* can do considerable damage to grain crops (Paulian & Popov 1980, Lodos 1981).

***Aelia* Fabricius, 1803**

In this genus, the body is longish with dark stripes on a straw-coloured ground, the head long, the second antennal segment not reaching the apex of the head, the front part of the pronotum with three long callosities, or "weals", the radial vein of the corium horny, raised. It is a largish genus containing more than twenty mainly Palaearctic species.

The *Aelia acuminata*-group (Wagner 1960)

Wagner (1960) examined the following species or forms: *A. acuminata* (Linnaeus, 1758); *A. alticola* Kiritschenko, 1914; *A. nasuta* Wagner, 1960; *A. satunini* Kiritschenko, 1930; *A. granum* Jakovleff, 1903; *A. demissa* Kiritschenko, 1914; *A. punctiventris* Horvath, 1911; *A. fieberi* Scott, 1874; *A. sibirica* Reuter, 1886; *A. henschi* Montandon, 1886; *A. turanica* Horvath, 1895; *A. klugi* Hahn, 1831. Voegelé (1968) considers *A. turanica* a synonym of *A. acuminata*.

The species in this group are small and slender (length range 6.6–10.8 mm: Wagner 1960), the bucculae straight, unarmed, and the juga often thickened behind; the upper border of the pygophore is relatively simple with at most a single median V-shaped notch; the parameres carry a broad membranous extension, the hypophysis is small, slender, curved and with a strong tooth; the superior processes although not identical in the different species conform to a similar plan (Voegelé 1968). From the description of the aedeagus given by McDonald (1966), Nearctic *A. americana* Dallas, 1851 appears to belong to this group; China & Lodos (1959) however report that *A. americana* has a body distinct from any other species of *Aelia*.

The *Aelia rostrata*-group (Wagner 1960)

Variability in the characters used in keys to species separations has been a source of much confusion in the genus on the species level. Wagner (1960) considered the following Palaearctic species or forms distinct: *A. melanota* Fieber, 1868; *A. obtusa* Fieber, 1868; *A. furcula* Fieber, 1868; *A.*

syriaca Horvath, 1903; *A. rostrata* Boheman, 1852; *A. cognata* Fieber, 1868; *A. germari* Küster, 1852; and *A. notata* Rey, 1888. He rejected *A. eminealkanata* Lodos, 1958 and *A. triticiperda* Pomel, 1889, considering the former to be a synonym of *A. syriaca* and the latter a synonym of *A. germari*. The status of *A. obtusa* remains to be settled: China & Lodos (1960) considered it a synonym of *A. melanota*. Brown (1962) and Voegelé (1968) have rejected *A. syriaca*, the latter author considering it a synonym, the former perhaps at most a geographical form, of *A. rostrata*.

The species in this group are larger and more robust than the preceding (length range 8.1–12.0 mm; Wagner 1960), the bucculae often armed with a tooth, and the juga without nodular thickenings. The upper posterior border of the pygophore is variable; it exhibits either three distinct notches or only one, the latter condition resembling that found in species of the *A. acuminata*-group. However, Wagner (1960) considered the character of the parameres as revealing the *A. rostrata*-group as a distinct unity within the genus *Aelia*: parameres in the *A. rostrata*-group longer than in the preceding, thicker distally, the membranous extension outwardly directed and the hypophysis short with a small tooth.

The *Aelia virgata*-group (Wagner 1960)

A small group containing the following species, *A. virgata* Klug, 1845; *A. albovittata* Fieber, 1868; *A. cribrosa* Fieber, 1868 (which seems to be close to *A. virgata*); and *A. contorta* Kiritschenko, 1929; all from the Palearctic region (Wagner 1960). The species are large (length range 8.4–10.8 mm, Wagner 1960), a darker colour than species in the preceding species-groups; the connexivum in whole or in part and the space between the connexivum and spiracles is dark or with dark markings; the bucculae lack a hump or knob. The parameres are without a membranous extension and altogether very different in appearance from those in other *Aelia* groups. The superior processes although not identical conform to a similar pattern in *A. virgata* and *A. albovittata* (Voegelé 1968).

The *Aelia frigida*-group (Wagner 1960)

This group contains only one species, *A. frigida* Kiritschenko, 1930, from the Palearctic region.

In *A. frigida*, the body is small (6.7 mm long in the one male examined by Wagner 1960), a darkish colour like the preceding, the bucculae in front with a rounded knob, the parameres lacking any leaf-like extension, the abdomen wider than the pronotum. The last feature is unique to *A. frigida* within the genus *Aelia*. The superior processes so far as we are aware have not been examined.

In the absence of material, we have been unable to examine the aedeagus in *A. frigida*.

***Neotiglossa* Kirby, 1837**

We have not attempted to follow the taxonomic literature concerning this genus. Kirkaldy (1909) lists at least 13 Palearctic and three Nearctic species. In *Neotiglossa*, the head is shorter compared with *Aelia*, strongly bent down, the second antennal segment extending beyond the apex of the head; the anterior part of the pronotum presents only one long weal; the radial vein of the corium is neither horny nor raised.

We have studied the aedeagus in Palearctic *N. bifida* (A. Costa, 1847) and *N. leporina* Puton, 1881.

MATERIAL AND METHODS

Material

Several persons and organizations kindly supplied the dry specimens on which our work was largely based: Natural History Museum, London (NHM); Entomology Department of Ege University, Bornova-Izmir, Turkey (EU);

Charles University, Prague, Czech Republic (CU). Some fresh *Aelia* material was obtained from Iran and elsewhere (*A. acuminata*) from the United Kingdom; specimens were identified using China & Lodox (1959), Wagner (1960) and Voegelé (1960, 1968).

Examination of the aedeagus

The genital capsule (pygophore) was removed from potashed males and again potashed prior to removal of the aedeagus. This treatment often resulted in partial and in some specimens complete inflation of the membranous conjunctiva. Structures were drawn to scale on graph paper with the aid of an eye-piece graticule at 50 \times magnification. For more detailed study, genital structures were mounted in Euparal and examined using a Zeiss photomicroscope equipped with ordinary light and phase-contrast optics.

STRUCTURE OF THE AEDEAGUS IN AELIINI

Fig. 1 gives a generalized picture of the aedeagus as seen in ventral view. It includes all the structures examined although deficiencies in certain structures occur in some aeliines.

Following Singh-Pruthi (1925), the aedeagus can be considered as comprising three parts; at the base is the phallosome; occupying an intermediate position is the largely membranous conjunctiva; distally there is the copulatory process. For the latter structure Singh-Pruthi (1925) used the term "vesica".

The phallosome can be subdivided into the following parts: basal thecal tube, thecal processes borne on the thecal tube, and distal thecal collar. The thecal tube is heavily sclerotized and contained within it is a specialized expansion of the gonoduct, the ejaculatory reservoir; the latter does not lend itself readily to investigation and was not examined in the present work. Thecal processes were present in all species examined; they show variability of taxonomic value, both in position and in form. The thecal collar extends from distal margin of the thecal tube; Gross (1976) gives the term thecal shield to this structure; the collar chamber partially encloses the conjunctiva. The narrow part of the phallosome between the collar and the thecal tube is here termed the thecal neck.

The thecal collar is made up of two separate parts which we term according to position dorsal and ventral collar domains. A dorsal collar domain was present and well developed in all aeliines examined; sometimes it exhibited an apparent lack of sclerotization in the middle region; to the differentiated middle region we give the term dorsal collar hinge, to the sclerotized parietal regions the term dorsal collar valves. The integument which lines the inner side of the dorsal collar domain appears to join the conjunctiva at or near the level of the thecal neck but in *A. virgata* seems to function as a component of the conjunctiva. The ventral collar domain is variable; sometimes it exhibits a pair of well developed lobes which we term here ventral collar valves.

The conjunctiva is largely membranous; in the resting aedeagus it occupies the chamber formed by the thecal collar; it is very variable and potentially useful as a source of characters on the species level. It mostly comprises one or two pairs of appendages with or without a dorsal median lobe; sometimes it bears a pair of sclerotized processes. The term paravesical processes is given here to the latter by virtue of their position on either side of the copulatory process. Terms previously used for similarly located sclerotic structures in Pentatomidae include median 'penal' lobes (McDonald 1966) and penial plates (Gross 1976); but the structures bearing this names vary considerably in form and it is possible that some are independent formations; some *Aelia* species (*rostrata*-group) are without paravesical processes.

The copulatory process consists of a slender sclerotized extension of the gonoduct; it bears the gonopore at or near its distal extremity; it exhibits wide differences in size and form on the species level.

It is considered likely that absences of ventral collar valves and paravesical processes where they occur in the genus *Aelia* are secondary and thus to be regarded as having taxonomic value as apomorphies.

Genus *Aelia*

1. *Aelia acuminata*-group

SPECIES STUDIED *Aelia acuminata*

Aelia acuminata

(Figs 2, 7, 12, 13)

PHALLOTHECA. The thecal tube (Fig. 2) is somewhat barrel-shaped with a pair of small, cone-shaped, thecal processes, the tube extends some way distally past the level of the thecal processes. The dorsal collar valves are prominent, their distal tips are widely separated and project beyond the distal border of the median hinge. The ventral collar domain is well developed with a pair of plate-like valves, squarish in shape, the gap between them narrow (Fig. 12). In the resting aedeagus, the ventral collar valves partially conceal the copulatory process, in the inflated aedeagus they are turned outwardly (Fig. 13).

CONJUNCTIVA. The conjunctiva exhibits a single pair of appendages and a prominent dorsal median lobe. The conjunctival appendages are relatively small, flattened structures, they are located between the dorsal and ventral collar domains and seem to be directly connected to the dorsal median

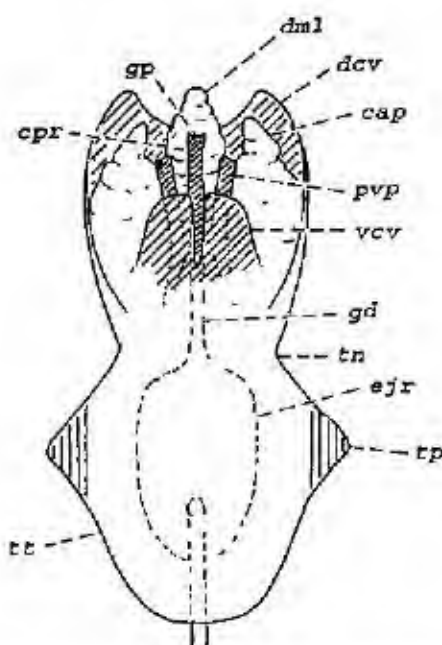


Fig. 1. Diagram showing the general structure of the aedeagus as seen in ventral view: cap - conjunctival appendage, cpr - copulatory process ("vesica"), dcv - dorsal collar valve, dm1 - dorsal median lobe of conjunctiva, cjr - ejaculatory reservoir, gd - gonoduct, gp - gonopore, pvp - paravesical process, tn - thecal neck, tp - thecal process, tt - thecal tube, vcv - ventral collar valve.

lobe by a connection near its base. The appendages are a squarish shape, the distal free corners slightly produced; their surfaces are smooth suggesting that little if any surface-area expansion occurs in the active aedeagus. The conjunctival dorsal median lobe (Figs 7, 12) is extensive, probosciform; the surface is thrown into numerous ring-like folds; the distal extremity sometimes presents a bilobed appearance; in one male the distal extremity revealed a balloon-like expansion (Fig. 12) but whether or not as an artefact we cannot be sure; Voegelé (1960) however described a similar mushroom-shaped expansion in *A. acuminata*.

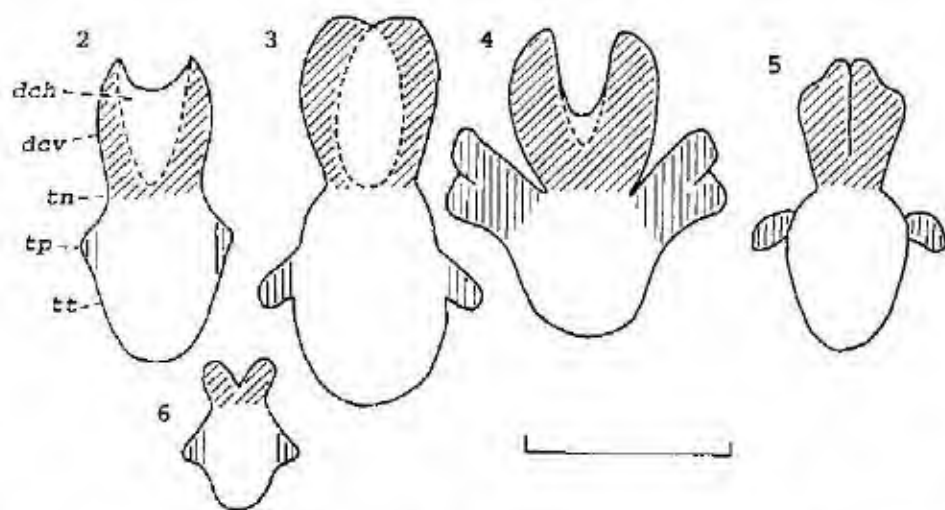
PARAVESICAL PROCESSES. The free distal extremities are somewhat flattened, blade-like structures; basally they seem to have connections both to the copulatory process and the dorsal median lobe. In the active aedeagus they turn outwardly; in so doing they expose the copulatory process and simultaneously press down on the ventral collar valves (Fig. 12).

COPULATORY PROCESS. This is a shortish (1 spec., 0.2 mm long) sclerotized structure; as seen in side view (Fig. 7), it is slightly S-shaped. The main axis seems to lack any twist; the distal extremity surrounding the gonopore is slightly flared; according to Voegelé (1960) it is divided to form two distinct lips.

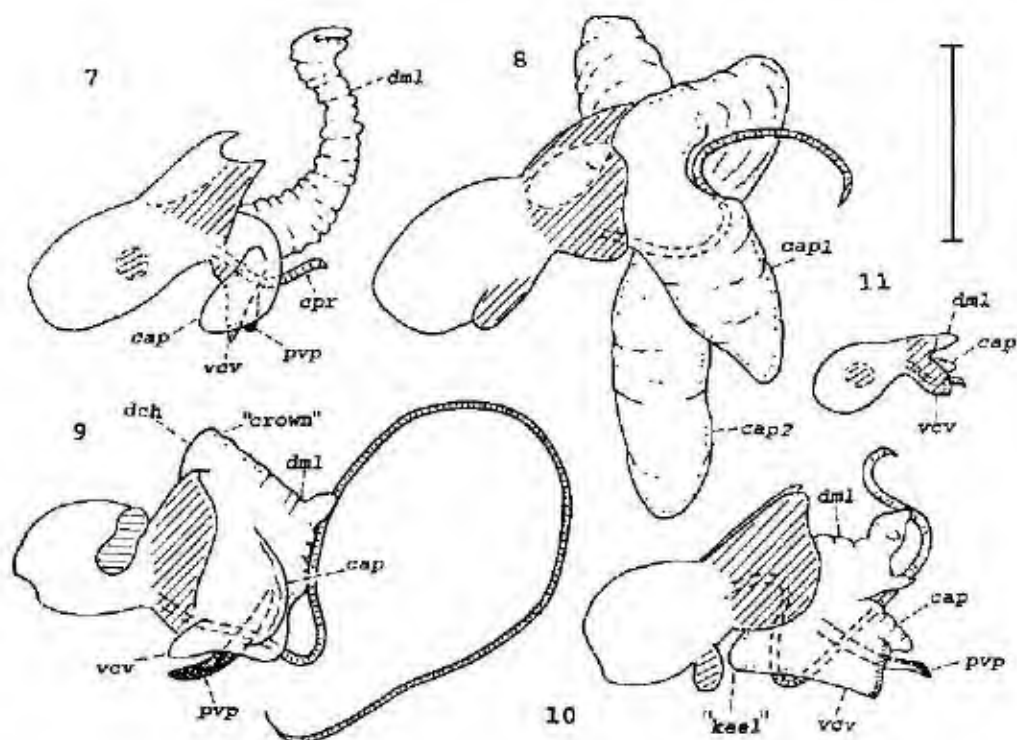
MATERIAL EXAMINED. *A. acuminata*: Turkey, 1 spec. Kozan, 4.v.1985 (this male had two pairs of sternal patches; see Staddon 1992) (EU); 1 spec. Afsin 6.vi.1973 (EU); 1 spec. Pamucak 14.vi.1977 (EU). We have also examined other males both from Turkey and the United Kingdom.

Aelia americana

The following notes are based on the description given of the aedeagus in *A. americana* by McDonald (1966): conjunctival appendages, a single pair, in the form of broad membranous lobes, rounded apically, balloon-like when fully inflated; dorsal median lobe large; paravesical processes



Figs 2-6. Structure of the phallosome in dorsal view. Fig. 2 - *Aelia acuminata* (Linnaeus); Fig. 3 - *A. rostrata* Rey; Fig. 4 - *A. virgata* Klug; Fig. 5 - *A. albevittata* Fieber; Fig. 6 - *Neottiglossa bifida* (A. Costa). dch - dorsal collar hinge; dev - dorsal collar valve; tn - thecal neck; tp - thecal process; tt - thecal tube. Scale line = 0.5 mm.



Figs 7-11. Structure of the aedeagus in lateral/dorso-lateral view; Fig. 7 - *Aelia acuminata* (Linnaeus); Fig. 8 - *A. rostrata* Rey; Fig. 9 - *A. virgata* Klug; Fig. 10 - *A. albobittata* Fieber; Fig. 11 - *Neottiglossa bifida* (A. Costa). cap - conjunctival appendage; cap1 and cap2 - first and second conjunctival appendages of one side; cpr - copulatory process; dch - dorsal collar hinge; dml - dorsal median lobe; pvp - paravesical process; vcv - ventral collar valve. Scale line = 0.5 mm.

(median 'penal' plates) small, thin, heavily sclerotized and fused to a wide common base; copulatory process (endophallic duct) sinuous, with a spout-like apex.

In general appearance and, in particular, in the form of the paravesical processes and copulatory process, *A. americana* and *A. acuminata* appear to be similar.

2. *Aelia rostrata*-group

SPECIES STUDIED. *A. rostrata*, *A. melanota*, *A. furcula*, *A. cognata*, *A. germari*.

The aedeagus of *A. rostrata* as noted previously was first described by Sisli (1964). It differs from *A. acuminata* most noticeably in the absence of ventral collar valves, absence of paravesical processes, absence of a conjunctival dorsal median lobe and by the fact of the presence of two pairs of conspicuous conjunctival appendages. Within the *A. rostrata*-group departures from the condition found in *A. rostrata* are most noticeable in the form of the conjunctiva and in the length of the copulatory process.

Aelia rostrata
(Figs 3, 8, 14)

PHALLOTHECA. The thecal tube (Fig. 3) is barrel-shaped; the thecal processes are short, somewhat stick-like, with parallel sides, directed basally; their distal ends are rounded. The dorsal collar valves (Fig. 3) are prominent, rounded distally; the median collar hinge is an oval shape, the distal end closed by the meeting of the dorsal collar valves in the mid line. The ventral collar domain (Fig. 13) is simple, greatly reduced; ventral collar valves are absent.

CONJUNCTIVA. The main structures are the two pairs of prominent membranous finger-like conjunctival appendages (Fig. 8); there is no differentiated conjunctival dorsal median lobe; paravesical processes are wanting. The uninflated appendages partially occupy the collar chamber in the resting aedeagus (Fig. 8).

COPULATORY PROCESS. This structure is longish (2 spec., 1.3 and 1.4 mm long), an S-shape when seen in side view (Fig. 8), with a slight twist about the principal axis; the distal extremity bearing the gonopore is slightly flared, somewhat scoop-shaped, the external surface with a granular appearance.

MATERIAL EXAMINED. *A. rostrata* Turkey: 1 spec., Kinkkale, 4.v.1979 (EU); 1 spec., Erzogh, 15.x.1965 (EU).

The *A. rostrata*-group: comparative observations

The phallosome presented the same appearance in all *rostrata*-group species examined. Variability in the dorsal collar domain and length of the copulatory process (cpr) are perhaps correlated; *A. germari* with the smallest collar had the shortest cpr (1 spec., 0.5 mm); *A. melanota* with the largest collar had the longest cpr (range 1.5 to 1.7 mm, 5 spec.). Intermediate were *A. furcula* (cpr 0.75 mm long, 1 spec.), *A. cognata* (cpr 1 mm long, 1 spec.), and *A. rostrata* (cpr 1.3 and 1.4 mm long, 2 spec.). Voegelé (1960) described the cpr of *A. furcula*; in this species it is peculiarly curved, the distal part strongly thickened and striated.

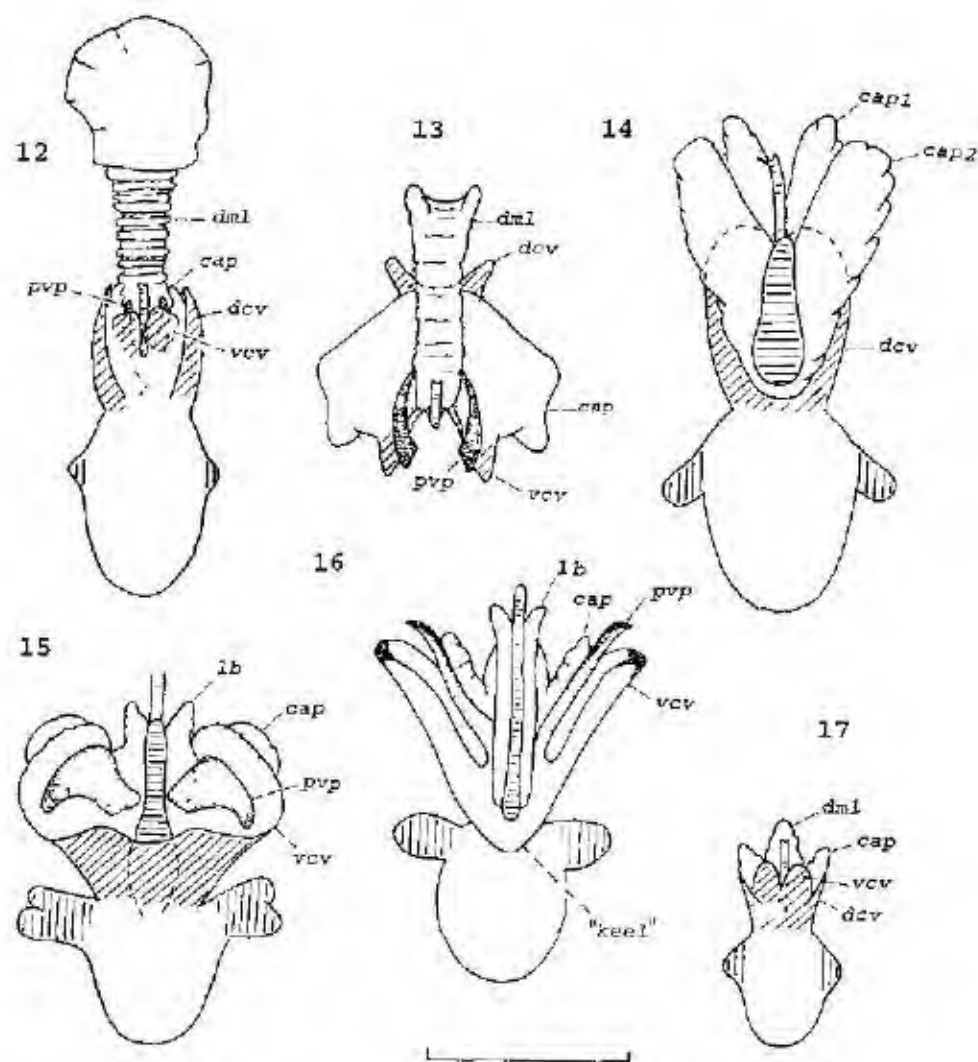
Our observations on the conjunctiva remain incomplete owing to the fact that complete inflation was attained in only two of the species examined (*A. rostrata*, *A. melanota*) but the following differences of interest were observed: in *A. melanota* the conjunctival first pair of appendages (cap1's) and the smaller second pair (cap2's) were voluminous and distinctly bilobed (as are the male genitalic superior processes; Voegelé 1968) contrasting with the simplicity of the corresponding appendages in *A. rostrata* (Fig. 8); in *A. cognata* the cap1's are sacciform, in *A. furcula* coniform, in *A. germari* appearing to bear a small branch on the ventral side (cap2's were not detected in the one male *A. germari* examined). In both *A. melanota* and *A. cognata* the conjunctiva was observed to bear a prominent dorsal median lobe.

MATERIAL EXAMINED. *A. germari* Sardinia, 1 spec., Macomer vi. 1931 (NHM). *A. furcula* Iran, 2 spec., Khomem 15.ix.1993 (coll. Abdollahi). *A. cognata* Turkey, 1 spec., Konya 22.iv.1964 (EU). *A. melanota* Iran, 5 spec., Kaboot, 1.v. 1992 (coll. Abdollahi).

3. *Aelia virgata*-group

SPECIES STUDIED. *Aelia virgata* and *A. albivittata*.

The many points of difference between them necessitate separate descriptions of the aedeagus in *A. virgata* and *A. albivittata*.



Figs 12-17. Structure of aedeagus in ventral view. Fig 12 - *Aelia acuminata* (Linnaeus), uncompletely inflated, exhibiting balloon-like expansion (perhaps an artefact) at distal extremity of conjunctival dorsal median lobe, Fig 13 - *A. acuminata* (Linnaeus), uncompletely inflated, the conjunctival appendages and paravesical processes turned outwardly, Fig 14 - *A. instrata* Rey, uncompletely inflated, Fig 15 - *A. virgata* Klug, partially inflated, Fig 16 - *A. albostriata* Fieber, partially inflated, Fig 17 - *Neobiglossa bifida* (A. Costa), partially inflated. cap - conjunctival appendage, cap1 and cap2 - first and second conjunctival appendages of one side, dev - dorsal collar valve, dml - dorsal median lobe, lb - conjunctival lobule, pvp - paravesical process, vcv - ventral collar valve. Scale line = 0.5 mm.

Aelia virgata
(Figs 4, 9, 15)

PHALLOTHECA. The thecal tube is relatively short, stoutish, lacking any extension beyond the level of the thecal processes (Fig. 4). The thecal processes are substantial and point apically; they are bilobed, the lobes leaving a cleft at the apex. The dorsal collar domain is well developed; the paired valves project dorsally, are widely separated, leaving a space for the membranous hinge. In side view (Fig. 9), it can be seen that the collar valves are directed dorsally; the median collar hinge is even turned basally. The valves of the ventral collar domain have rounded extremities (Fig. 16).

CONJUNCTIVA. There is a single pair of conjunctival appendages (Fig. 16); they are rounded, somewhat cushion-shaped, and not sharply demarcated from the ventral collar valves; their surfaces are wrinkled. The conjunctival dorsal median lobe bears a double row of short finger-like lobules; the latter presumably grip and help control positional movements of the copulatory process. Dorsally the dorsal conjunctival median lobe assumes the form of a dome-shaped "crown" (Fig. 9); the dorsal collar hinge appears to make a contribution to this formation. The paravesical processes (Figs 9, 16) are heavily sclerotized, somewhat spine-shaped; they point away from the copulatory process in the active aedeagus.

COPULATORY PROCESS (Fig. 9). In *A. virgata*, the cpr is exceptionally long (2 spec., 3.1, 3.4 mm long), thread-like, with one sharp U-turn near the base; distally it forms an extended loop while remaining in the same plane. The apical extremity bearing the gonopore is drawn out into an acutely pointed process (gonoporal process; Dupuis 1970); the external surface presents both longitudinal striations and surface granulation.



Fig. 18. Spermatheca of *Aelia ulhovittata* Fieber. Spermathecal dilatation arrowed. Scale line = 0.2 mm.

MATERIAL EXAMINED: Turkey 2 spec., Gordes, 20.vii.1977, Gramineae (BU); Eregli, 10.v.1957 (EU); Iran 1 spec., Kabontar-Ahang 10.ix.1992 (coll. Abdollahi).

Dimensions of male copulatory process and female spermathecal proximal duct in *A. virgata*

Singh-Puri (1925) noted that lengths of male and female copulatory structures (copulatory process in male, spermathecal proximal duct in female) in Pentatomidae were similar but he provided no quantitative data. We have obtained the following measurements for these structures in *A. virgata*.

Males, 2 spec.: length of copulatory process 3.1 and 3.4 mm; in both spec. outer diameter towards free extremity 0.025 mm, outer diameter towards base 0.050 mm.

Female, 1 spec.: length of spermathecal proximal duct 2.7 mm, the outer diameter 0.075 mm, the inner diameter 0.060 mm.

Evidently, the spermathecal proximal duct is adapted to receive the male copulatory process during copulation (Ludwig 1926, Bonhag & Wick 1953, Gaffour-Bensebbane 1993, 1994).

Aelia albovittata

(Figs 5, 10, 16)

PHALLOTHECA. The thecal tube (Fig. 5) is somewhat vase-shaped; the thecal processes are prominent, wider in the middle than at either extremity, almost ovoid; they are located at some distance from the thecal neck. The dorsal thecal collar is well developed, directed apically; the collar valves appear to meet in the middle to the exclusion of any dorsal collar hinge. The ventral collar domain (Figs 10, 17) is prominent; it presents a median, basally directed, membranous keel-like extension; the paired ventral valves are directed apically; their distal extremities are squarish, partially sclerotized.

CONJUNCTIVA. The conjunctival appendages, a single pair, are small, wholly membranous, coniform structures, their tips pointed (Figs. 10, 17). The dorsal conjunctival median lobe bears lobules; we have observed a single median lobule, itself bearing branches, and below that a pair of smaller lobules. There are differences in the pattern presented by the lobules in *A. albovittata* and *A. virgata*.

COPULATORY PROCESS (Fig. 10). It is of intermediate length (1 spec., 1.1 mm long), presents two double-bends, and appears to lack any axial twist; the distal extremity bearing the gonopore is acutely tapered, or chisel-edged.

MATERIAL EXAMINED: Turkey c spec.: 1 spec. Yamanlar 24.v.1973 from Gramineae, Det. N. Lodos 1973 (EU); 1 spec. Pozanti 1.v.1984 from Gramineae (EU); 1 spec. Sogut 25.vi.1980, from Gramineae (EU).

Condition of the spermathecal dilatation in *A. albovittata* (Fig. 18)

In all *Aelia* species so far as is now known (Voegelé 1960, *A. acuminata*, *A. cognata*, *A. germari*; our observations, *A. furcula*, *A. melanota*, *A. rostrata*, *A. albovittata*, *A. virgata*; McDonald 1966, *A. americana*) the spermatheca conforms to the usual pentatomid type with distal bulb (the spermatheca proper), pumping region, distal duct, dilatation with enclosed "rod", and proximal duct (McDonald 1966). The dilatation it seems functions as an organ of storage and digestion for excess materials, including sperm, which the male transfers to the female during copulation (Berlese 1898, 1899, Handlirsch 1900, Kon et al. 1993).

In the species of *Aelia*, the spermathecal bulb bears a pair of tubuli, usually with the one tubulus longer than the other (the tubuli are similar in *A. albovittata*); the spermathecal dilatation is usually extensive; in *A. virgata* the entire system is greatly extended. Here we report the interesting finding that in *A. albovittata* the spermathecal system exhibits reduction most conspicuously in the dilatation and its enclosed rod (Fig. 18). The dilatation it seems is vestigial, presumably

without function. Tamanini (1959) describes a similar condition in the spermatheca of some Car-pocorinae (*Dolycoris* Stål, 1872, *Eudolycoris* Tamanini 1959).

MATERIAL EXAMINED. Turkey, 1 spec. Bigadif, 17.v.1971 (EU); Turkey, 1 spec. Bosika Bay, 1927 (NHM); Turkey, 1 spec. Ankara, 14.viii.1947 (NHM).

Genus *Neottiglossa*

SPECIES STUDIED. *Neottiglossa bifida* and *N. leporina*. McDonald (1966) has given a description of the aedeagus in Nearctic *N. trilineata* Kirby, 1837.

In both *N. bifida* and *N. leporina* the aedeagus was small in size and examined with difficulty; conjunctival inflation was probably incomplete. Spine-shaped structures, perhaps paravesical processes, were observed in slide-preparations of the aedeagus (*N. leporina*) but their independent existence could not be confirmed by dissection.

The aedeagus of *Neottiglossa bifida* was selected for the following description of gross morphology.

Neottiglossa bifida (Figs 6, 11, 17)

PHALLOTHECA. The thecal tube (Fig. 6) is barrel-shaped; the thecal processes are cone-shaped, like those of *A. acuminata*; the dorsal collar valves have rounded extremities with a V-shaped gap appearing to replace any median hinge; the ventral collar domain (Figs 11, 18) is well developed with a pair of conspicuous ventral collar valves.

CONJUNCTIVA. Figs 11, 17. The conjunctiva presents a single pair of coniform conjunctival appendages together with a prominent but smallish, cone-shaped, dorsal median lobe (a slide preparation of the aedeagus of *N. leporina* revealed the presence of minute papillae on the dorsal median lobe).

PARAVESICAL PROCESSES. These structures were looked for but not convincingly found; we cannot conclude that they are absent.

COPULATORY PROCESS. Shortish (1 ex, approx 0.2 mm long), straight when viewed from above; with a single shallow bend when seen from the side; the extremity surrounding the gonopore tapered, ending in a point.

MATERIAL EXAMINED. *N. bifida*, Turkey, 1 spec., Seferihisar, 19.v.1970, N. Lodos det.(EU); *N. leporina*; 2 spec., Čenkov - Slovakia mor. 10.vi.1962 (coll. P. Stys) (CU). Other specimens were examined in an attempt to clarify anatomical details without adding anything new.

Neottiglossa trilineata

The following description is slightly adapted from the account given by McDonald (1966): thecal tube stout, thecal processes knob-like, the dorsal collar domain consisting of two pointed valves with a wide U-shaped depression between them; one pair of membranous conjunctival appendages, apically broadly rounded; dorsal median conjunctival lobe large, voluminous; paravesical processes sclerotized, cylindrical, curved inwardly, fused basally along their ventral margins and connected to the "sub-apex" of the copulatory process by a thickened arm on each side.

In this description we find several points of similarity with *Aelia acuminata*: form of thecal collar, development of dorsal median lobe, form of copulatory process, general (but not precisely) similar form and attachments of paravesical processes. Indeed, *N. trilineata* seems to be closer to *A.*

acuminata than to the two Palearctic species of *Neottiglossa* examined. Discrimination might be aided by the presence of papillae or otherwise on the conjunctival dorsal median lobe.

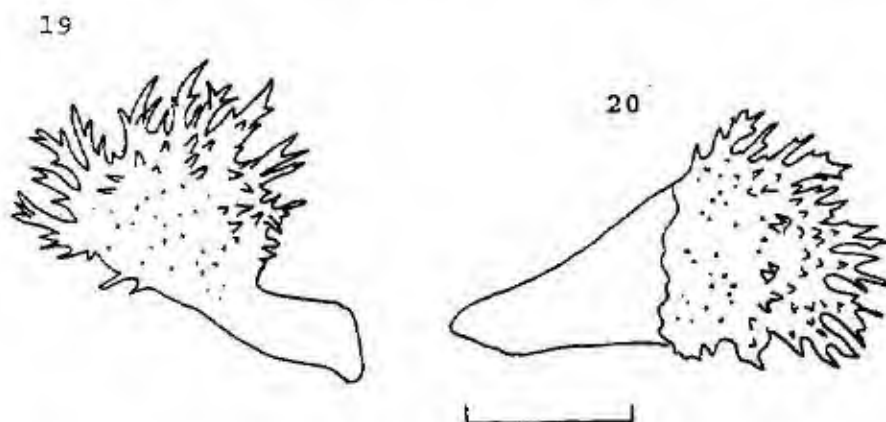
DISCUSSION

The genus *Aelia* contains four species groups which, so far as concerns the three groups here examined, differ widely from one another in the character of the aedeagus; but while the species groups might be considered distinct we are unable to regard the question of the unity of the genus as settled.

The position of the *Aelia acuminata*-group is of some interest; it seems to bear a close relationship to *Neottiglossa* in several points of similarity, especially in the shape of the pygophore (Davidova-Vilimová 1991), construction of the parameres, construction of the male genitalic superior processes (Voegelé 1968; this paper Figs 19, 20), and general character of the aedeagus. However, it is possible that the similarities involve plesiomorphies of limited taxonomic value, only future work can tell.

The species forming the *Aelia rostrata*-group are distinguished by the form of the thecal tube, thecal processes, and thecal collar, the manner of organization of the conjunctiva, the general form of the copulatory process, and by the fact that ventral collar lobes and paravesical processes are wanting. In the only alteration so far made to Wagner's (1960) classification of the species of *Aelia*, Voegelé (1968) split the *rostrata*-group owing to differences in the character of the superior processes coupled with minor differences in the character of the parameres and anterior border of the male genital cavity; he retained *A. melanota*, *A. rostrata* and *A. cognata* in the *rostrata*-group and established a *germari*-group comprising *A. germari*, *A. furcula* and *A. notata*. However, for reasons of the close similarity of the aedeagus, we suggest that the species forming Wagner's (1960) *rostrata*-group should remain together; in short, the *Aelia rostrata*-group should be considered a natural one while allowing internal division along the lines proposed by Voegelé (1968).

The species examined in the *Aelia virgata*-group are abundantly distinct from the *A. acuminata* and *A. rostrata* groups; future work might well reveal that the aedeagus in this group is more akin



Figs 19-20. Male genitalic superior process. Fig. 18 - *Neottiglossa leporina* Puton; Fig. 19 - *N. bifida* (A. Costa). Scale line = 0.1 mm.

to that of Pentatomidae outside the Aelini. For *A. virgata* and *A. albobittata*, unifying features include the general structure of the conjunctiva, the presence of paravesical processes, both coupled with the structure of the parameres (Wagner 1960) and superior processes (Voegelé 1968). However, in their many points of difference, *A. virgata* and *A. albobittata* might be considered as belonging to separate genera. Points of difference between them include the form of the thecal processes, thecal collar, and paravesical processes, the form and length of the copulatory process, the manner of elaboration of the conjunctiva, and the form of the dorsal median lobe and ventral collar domain.

It might now be considered that the genus *Aelia* as presently defined is somewhat artificial, perhaps paraphyletic, comprising as it does species and groups with such conspicuous differences in aedeagal structure. However, while it is evident that the character of the aedeagus is very useful taxonomically in subdivision, it has to be asked whether it tends to push widely apart groups that ought to remain together. This question cannot be answered on the basis of the information presently available, however, a taxonomic unity is suggested by the condition of the spermathecal bulb with its two tubuli, usually, as previously noted, with one tubulus longer than the other.

Nomenclatural considerations

The assignment of the ventral collar domain to the theca is clearly open to dispute, as a question of anatomical fact, but the question is of little importance in a comparative study provided that consistency of nomenclature is maintained. A difficulty of interpretation presented by *A. albobittata* is that the keel-like extension of the ventral collar domain is extensively membranous and on that basis some authors might consider it a conjunctival formation.

Some functional considerations

We can only speculate on the problem of the factors that have promoted functional and structural changes in the aedeagus in Aelini. The function of paravesical processes, for example, remains unclear, they are not always essential as is shown by their absence in *Aelia rostrata*-group species. Two suggestions are, firstly, that they provide a mechanism for locking the aedeagus to the external female genitalia during copulation (Singh-Pruthi 1925) and, secondly, that as levers, by pushing outwardly the conjunctival appendages and ventral collar lobes, they provide a mechanism for freeing the copulatory process in the active aedeagus (Figs 13, 15), but it would be premature to correlate their absence in the *Aelia rostrata*-group with the absence of well-developed ventral collar lobes since comparable processes are present in many pentatomids which otherwise lack a thecal collar (McDonald 1966, Gross 1976).

The copulatory process shows a 'tendency' to lengthening in many groups of Pentatominae, in the genus *Aelia* this tendency is evident in the *rostrata* and *virgata* species-groups. Although lengthening might involve an allometric component the great difference observed in *A. virgata* and *A. albobittata* obviously defies a simple allometric explanation.

Sperm competition provides one mechanism for promoting change in copulatory structures (Thornhill & Alcock 1983, Eberhard 1985). Many Pentatomidae engage in polyandrous as well as in polygamous behaviour, the list includes *Murgantia histrionica* (Hahn, 1834) (Lanigan & Barrows 1977), *Podisus modestus* (Dallas, 1851) (Tostowaryk 1971), *Nezara viridula* (L., 1758) (Mitchell & Mau 1969) and *Plautia stali* Scott, 1874 (Mau & Mitchell 1978), but we are not aware of any comparable study on the species of *Aelia*. For a female, there will be an advantage in polyandry if she is unable to obtain sufficient sperm from one mating to realise her full reproductive potential (Mau & Mitchell 1978), but she will also gain if several matings are required to fill the spermathecal dilatation.

The work of Arnqvist (1998) commentary by Gwynne (1998) indicates that male genital evolution proceeds more rapidly in groups in which females mate several times than in related groups in which females mate only once

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Effect of some environmental factors on structure of bug taxocoenoses (Heteroptera) in floodplain forest epigaeon of the Danube region

Oľga ŠTEPANOVICOVÁ & Peter DEGMA

Department of Zoology, Faculty of Science, Comenius University,
Mlynská dolina B-1, SK-842 15 Bratislava, Slovakia

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Abstract. The authors investigated the effects of some environmental factors on the qualitative and quantitative structure of taxocoenoses of Heteroptera in epigaeon of floodplain forests of the Danube region in Slovakia. On the basis of research conducted between 1991 and 1996 in 8 study areas 84 bug species were found whose mean abundance in the total area of interest and for the whole period of investigations was 6.23 ex. m⁻². It was shown that of the 9 tested variables by the PCA and CCA method the most significant are moisture of the soil and of the leaf litter. The values of dominance, mean abundance and constancy confirmed that in epigaeon of the floodplain forest prevail the populations of 5 characteristic species, namely *Scolopostethus affinis* (Schilling, 1829), *S. thomsoni* Reuter, 1874, *Dryinus brunneus* (F. Sahlberg, 1848), *D. ryan* Douglas et Scott, 1865 and *Leptogaster limbatus* (Geoffroy, 1785). The construction works and water service activities, which resulted in a gradual aridisation and subsequent ruderalisation of floodplain forests, caused an increase in the species number by their penetration from the surrounding meadow, field and ruderal communities.

Taxocoenoses, floodplain forest, epigaeon, environmental factors, Heteroptera, Slovakia

INTRODUCTION

At present, floodplain forests represent threatened habitats all over Europe. They are situated along larger rivers and their gradual disappearance is caused mainly by regulation of streams and by build-up of waterworks. This also applies to the floodplain forests along the Danube in the territory of Slovakia that have been affected by the build-up of the waterwork at Gabčíkovo over the past two decades. The remnants of floodplain forests along the Danube in Slovakia are unique within Central Europe and the whole Danube region, therefore they are registered according to the Ramsar Convention in the world list of internationally important wetlands.

In our previous studies (Štepanovičová 1995, 1997) we investigated epigaic Heteroptera of floodplain forests along the Danube from the aspect of changes occurring in the structure of their taxocoenoses due to technical activities in this region. In the present report the effect of some environmental factors on the structure of taxocoenoses of Heteroptera in the epigaeon of floodplain forests was assessed and we also investigated the effect of environmental variables on the occurrence of some important species.

STUDY AREA

The research of taxocoenoses of epigaic Heteroptera was performed in 1991–1996 in the floodplain forests of the Danube region in 8 study areas (SA) in the following localities: Podunajské Biskupice (SA 1), Čunovo (SA 2), Dobrohošť (SA 3), Bodíky (SA 4), Trstená na Ostrove (SA 5), Gabčíkovo (SA 6), Kľáčovec (SA 7) and Čiešov (SA 8). As shown in Fig. 1, SAs 1 and 2 are situated in the upper part of the area of interest, in the vicinity of the newly built water reservoir, SAs 3, 4, 5 and 6 are situated in the region of the inland delta of the Danube in an area that

is localised between the diversion channel and the original riverbed of the Danube, and SAs 7 and 8 are situated beneath the water power station at Gabčíkovo along the original riverbed of the Danube.

Floodplain forests which comprise the above 8 study areas are situated along the Danube over 66 km (river kilometres 1864 – 1798) and belong to the association *Salici-Populetum*, alliance *Salicion albae* (Oberd. 1953) Th. Müller et Gors (1958). They have different character that is affected not only by technical activities over the past decades. According to Jurko (1958), within the association *Salici-Populetum* (Tx. 1931) Meyer Drees 1936 in the Danube region 4 variants occur, and, on the basis of adequate groundwater depth, height and duration of inundations, and the level of the relief they are classified from the wettest to the driest variant. The latter occurs in SAs 1 and 2 in which the floodplain forest is studied in the direct vicinity of the xerothermic community *Asparago-Grataegietum* Jurko (1958) Mucina et Maglocký (1985). These 2 areas, in contrast to the other 6 SAs, were not inundated by superficial floods and also the level of groundwater was low. Only in the last 3 years, in connection with the build-up of the water reservoir at Čunovo, an elevation of groundwater level was recorded, along with, to a certain degree, the revitalisation of the forest community.

In the whole area of interest there was a prevalence of arenaceous eutric fluvisol, only in SA 3 there was a typical eutric fluvisol, and in SA 5 there was a clayey eutric fluvisol (Cambel 1995).

METHODS

Material of Heteroptera was collected by the square method combined with sifting. In each SA, at about 1-month intervals, from May to October, the material was collected from the leaf litter and the upper part of soil from 16

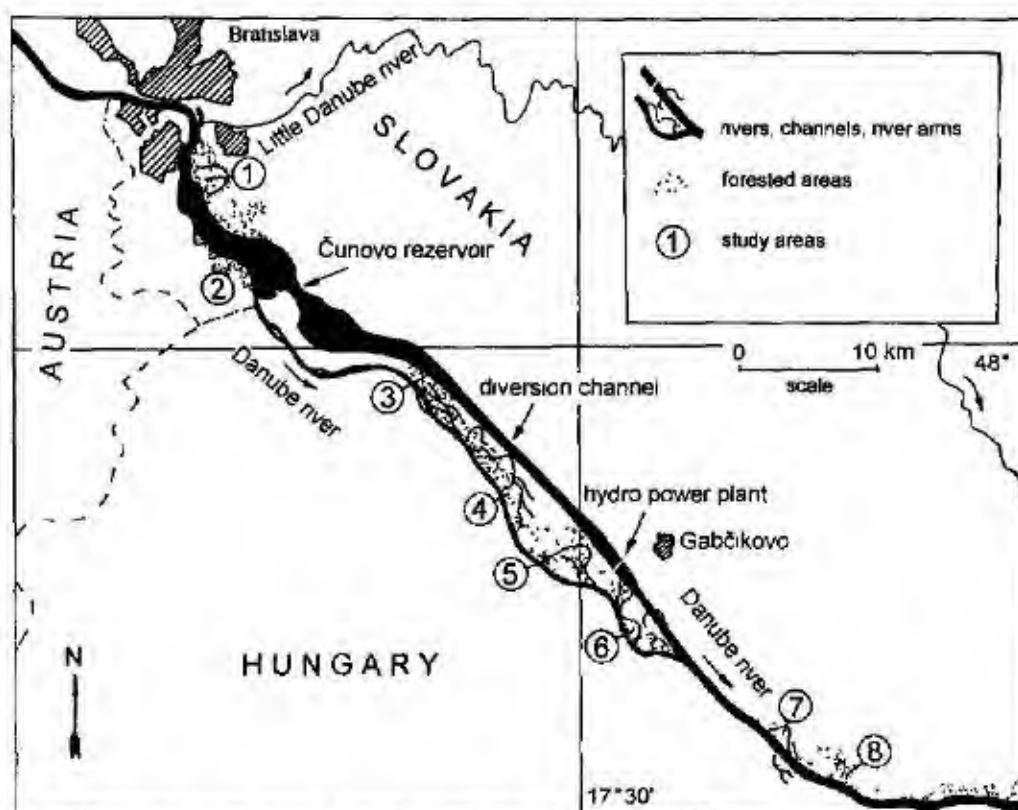


Fig. 1. Outline of the Gabčíkovo hydro-power plant area with the study areas location.

squares. Each square comprised 25×25 cm, i.e. altogether an area of 1 m², and this represented one sample. The material thus obtained was selected in xerolector. The numbers of individuals of the occurring species (Table 1) are expressed as values of mean annual abundance per 1 m². In SAs 1, 2, 4, 5, 6 and 8 the collections were performed from 1991 to 1996, in areas 3 and 7 from 1993 to 1996.

The material of Heteroptera is deposited at Department of Zoology of Comenius University in Bratislava.

Shannon–Weaver's species diversity and evenness indices were count on the basis of mean annual abundance of species and by using natural logarithms (in Poole 1974). Coenoses in the 8 SA were clustered using the method of complete linkage (clustering algorithm in Podani 1990) on the basis of presence of the respective taxons of Heteroptera, or on the basis of their mean abundance per year. In the former case, in the course of hierarchical classification the Soerensen index was used, while in the latter case the Wishart quantitative index of ecenotic similarity (algorithms for both of coefficients in Podani 1993, Wishart's index is mentioned as *Similarity ratio*). The mean annual abundance of every taxon was a basis also for the ordination of the 8 coenoses by the method of standardised principal components analysis (PCA). Classifications and ordinations were performed by computer programs ncl and princorp (Podani 1993). The association of the respective taxons with the environmental variables was analysed using the method of canonical correspondence analysis (CCA), taking into account the values or categories of the following nine environmental variables: monthly mean values of soil moisture in a horizon to a depth of 0.1 m (not measured in SA 1 and SA 8, and in SA 2 measured only from July 1995, otherwise the measurements were interrupted only exceptionally due to inaccessibility of the respective SA), soil pH, soil CaCO₃ content, humus content of soil (measured once in each SA), mean monthly air temperature, sum of monthly water precipitation (measured on one site for the total area), year and month of sampling, study area. The respective taxons in the analysis were represented by their abundance per 1 m² in sample. With respect to the coverage of samples by measurements of soil moisture, 186 samples were entered in this analysis. During analysis the variables were selected by the technique of forward selection. CCA was performed using the program Canoco (for Breuk 1993).

RESULTS

Between 1991 and 1996, 1,519 individuals of Heteroptera were collected (1,332 imagoes and 187 nymphs) belonging to 84 species. The value of their mean abundance in the whole studied area and for the whole period of investigation was 6.23 ex. m⁻².

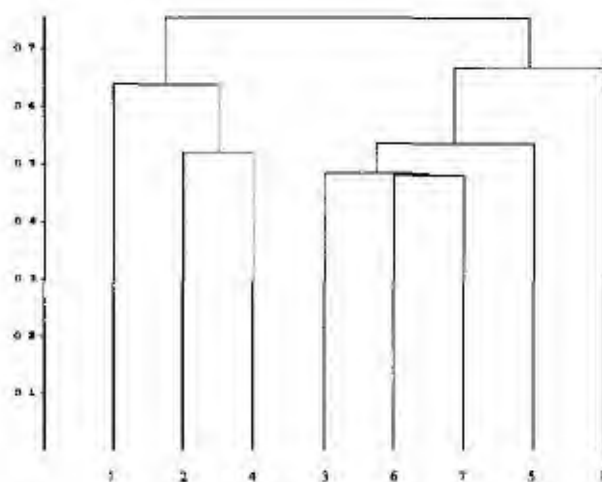


Fig. 2 Result of the eight coenoses of Heteroptera classification based on the presence of taxons (Complete linkage clustering method, Soerensen's index of similarity, numbers of study areas according to Tab. 1, vertical axis = dissimilarity level)

Tab. 1. List of Heteroptera taxons with values of mean annual abundance (upper values), dominance (lower values), constancy (Co, EC = eueconstant, C = constatit, AS = accessario, Ad = accidental species) (* = selected species, bold = characteristic species)

Nr	Taxon / Study area	1	2	3	4	5	6	7	8	Co
*1	<i>Ceratozonibus coleopratus</i> (Zetterstedt, 1819)			0.16 0.29		0.16 1.56		0.83 2.87	1.75 7.22	AS
2	<i>Ilyocoris cunicoides cunicoides</i> (Linnaeus, 1758)								0.25 1.03	Ad
3	<i>Hydrometra stagnorum</i> (Linnaeus, 1758)				0.16 0.25			0.16 0.55		Ad
4	<i>Gerris lacustris</i> (Linnaeus, 1758)		0.25 0.82		0.16 0.25	0.16 1.56				AS
5	<i>Salda opacula</i> (Zetterstedt, 1839)								0.25 1.03	Ad
6	<i>Alloeorhynchus flavipes</i> (Fieber, 1836)	0.16 0.43	0.25 0.82							Ad
7	<i>Himacerus mirmecoides</i> (Costa, 1834)				0.16 0.25					Ad
8	<i>Nabis punctatus</i> (Costa, 1943)			0.16 0.29	0.16 0.25					Ad
9	<i>Nabidae</i> nymphae diversae					0.33 3.22				Ad
10	<i>Adelphocoris aetionis</i> (Fabricius, 1775)					0.16 1.56				Ad
11	<i>Lygus rugulipennis</i> Pappius, 1911				0.16 0.25		0.16 0.79			Ad
12	<i>Agnocoris reclusae</i> (E. Wagner, 1949)			0.16 0.29						Ad
13	<i>Acalypta nigra</i> (Fallen, 1807)	0.25 0.82								Ad
14	<i>Derephysia foliacea</i> (Fallen, 1807)			0.16 0.29						Ad
15	<i>Lastacantha capucina</i> (Germar, 1836)							0.50 1.73		Ad
16	<i>Tingis ampliata</i> (Herrich-Schaeffer, 1830)				0.30 0.78					Ad
17	<i>Catoplatys carthusianus</i> (Goere, 1778)				0.33 0.52		0.16 0.79			Ad
18	<i>Onicostola scapularis</i> Fieber, 1844						0.16 0.79			Ad
19	<i>Dictyla humuli</i> (Fabricius, 1794)				0.83 1.30					Ad
20	<i>Aradus depressus depressus</i> (Fabricius, 1794)						0.16 0.79			Ad
21	<i>Aradus distinctus</i> Fieber, 1861		0.50 1.64	0.33 0.59	0.16 0.25				0.25 1.03	AS
22	<i>Aneurys avenius</i> (Dufour, 1883)	0.16 0.43								Ad
23	<i>Aradidae</i> nymphae diversae	0.33 0.88	0.50 1.64	0.16 0.29					0.50 2.06	AS
24	<i>Piesma capitatum</i> (Wolf, 1804)		0.50 1.64		0.16 0.25					Ad
25	<i>Piesma maculatum</i> (Laporte, 1832)	0.50 1.34		0.50 0.89	0.33 0.52			0.50 1.73		AS
26	<i>Cymus clavicornis</i> (Fallen, 1807)					0.16 1.56				Ad

Tab. 1 Continued

Nr	Taxon / Study area	1	2	3	4	5	6	7	8	Co
*27	<i>Holcocranum saturejae</i> (Kolenati, 1845)			0.33 0.59		0.50 4.88	0.16 0.79	0.33 1.14		AS
28	<i>Platypiax salviae</i> (Schilling, 1829)		0.25 0.82							Ad
29	<i>Metopopax origani</i> (Kolenati, 1845)	0.33 0.88	0.25 0.82	0.16 0.29	0.50 0.78	0.16 1.56				C
30	<i>Oxycaenus pallens</i> (Herrich-Schaeffer, 1850)				0.33 0.52					Ad
31	<i>Plinthisus brevipennis</i> (Latreille, 1807)		0.50 1.64							Ad
32	<i>Stygnocoris fuligineus</i> (Geoffroy, 1785)	0.16 0.43	0.25 0.82							Ad
33	<i>Stygnocoris sabulosus</i> (Schilling, 1829)		0.25 0.82			0.16 1.56	0.16 0.79			AS
34	<i>Stygnocoris ruscus</i> (Fallén, 1807)			0.16 0.29		0.16 1.56				Ad
35	<i>Tropistethus holosericeus</i> <i>holosericeus</i> (Scholtz, 1845)	0.33 0.88			0.75 1.18			0.16 0.55		Ad
36	<i>Ischnocoris hemipterus</i> (Schilling, 1829)		0.25 0.82		0.16 0.25					Ad
37	<i>Scolopostethus affinis</i> (Schilling, 1829)	1.33 3.56	0.25 0.82	2.16 3.86	9.66 15.15	2.16 21.09	3.16 15.51	4.50 15.57	2.25 9.28	EC
*38	<i>Scolopostethus pictus</i> (Schilling, 1829)	0.33 0.88			0.33 0.52			0.50 1.73	1.00 4.12	AS
*39	<i>Scolopostethus pilosus</i> Reuter, 1874				0.16 0.25		0.33 1.62		0.50 2.06	Ad
40	<i>Scolopostethus thomsoni</i> Reuter, 1874		0.50 1.64	2.50 4.47	6.00 9.41	0.16 1.56	2.00 9.82	1.50 5.19		C
41	<i>Scolopostethus</i> spp. nymphae			0.66 1.18			0.16 0.79	0.16 0.55		AS
*42	<i>Eremocoris podagricus</i> (Fabricius, 1775)	3.75 10.03	0.50 1.64	2.50 4.47	0.16 0.25		0.50 2.45	0.50 1.73	0.50 2.06	EC
43	<i>Gastrodes grossipes</i> (De Geer, 1773)		0.50 1.64							Ad
44	<i>Drymus brunneus</i> (F. Sahlberg, 1848)	1.50 4.01		31.16 55.65	26.00 40.78	2.00 19.53	6.83 33.53	11.33 39.19	10.25 42.27	EC
45	<i>Drymus ryeli</i> Douglas et Scott 1865		0.25 0.82	0.83 1.48	5.83 9.15	0.16 1.56	1.00 4.91		0.75 3.09	C
46	<i>Drymus sylvaticus</i> (Fabricius, 1775)	0.16 0.43			0.16 0.25			0.16 0.55		AS
47	<i>Rhyparochromus lynceus</i> (Fabricius, 1775)				0.16 0.25	0.16 1.56				Ad
48	<i>Rhyparochromus quadratus</i> (Fabricius, 1798)	0.16 0.43								Ad
*49	<i>Rhyparochromus alboacuminatus</i> (Goeze, 1778)	0.33 0.88		0.33 0.59	0.16 0.25	0.83 8.11				AS
50	<i>Rhyparochromus vulgaris</i> (Schilling, 1829)			0.16 0.29						Ad
51	<i>Pertrechus gemiculatus</i> (Hahn, 1832)			0.16 0.29						Ad
52	<i>Pertrechus gracilicornis</i> Puton, 1877		0.25 0.82	0.16 0.29						Ad
53	<i>Pertrechus nubilus</i> (Fallén, 1807)						0.16 0.79	0.16 0.55		Ad

Tab. 1 Continued

Nr.	Taxon / Study area	1	2	3	4	5	6	7	8	Co
*54	<i>Megalonotus chiragra chiragra</i> (Fabricius, 1794)	0.16 0.43	0.50 1.64	0.16 0.29	0.50 0.78	0.16 1.56	0.50 2.45	0.16 0.55		BC
55	<i>Megalonotus praetextatus</i> (Herrich-Schaeffer, 1835)	0.33 0.88								Ad
56	<i>Megalonotus sabulicola</i> (Thomson, 1870)	0.16 0.43		0.33 0.59	0.33 0.52					AS
*57	<i>Trapezonotus arenarius</i> (Linnaeus, 1758)	0.33 0.88	1.00 3.28				0.16 0.79			AS
58	<i>Trapezonotus dupar</i> Stahl, 1872	0.16 0.43								Ad
59	<i>Emblethis denticollis</i> Horváth, 1878	0.50 1.34		0.50 0.89		0.16 1.56	0.16 0.79	0.16 0.55		C
60	<i>Emblethis griseus</i> (Wolff, 1802)		0.50 1.64	0.16 0.29	0.16 0.25		0.16 0.79			AS
*61	<i>Emblethis verbascae</i> (Fabricius, 1803)	0.16 0.43	0.25 0.82		1.66 2.60		0.33 1.62			AS
62	Lygaeidae nymphae diversae		0.25 0.82	4.16 7.43	5.83 9.15	1.00 9.77	1.16 5.69	2.66 9.20	0.50 2.06	BC
*63	<i>Pyrrhocoris apterus</i> (Linnaeus, 1758)	2.27 6.07						0.16 0.55		Ad
64	<i>Coreus marginatus marginatus</i> (Linnaeus, 1758)	0.16 0.43								Ad
*65	<i>Arenocoris falleni</i> (Schilling, 1829)	1.00 2.67			0.16 0.25		0.16 0.79	0.33 1.14		AS
66	<i>Ceraleptus lividus</i> Stein, 1858	0.33 0.88								Ad
67	<i>Ceraleptus gracilicornis</i> (Herrich-Schaeffer, 1835)	0.50 1.34								Ad
68	<i>Coptosoma scutellatum</i> (Geoffroy, 1785)	0.16 0.43								Ad
69	<i>Thyreoxenus scarabaeoides</i> (Linnaeus, 1758)	0.66 1.77		0.16 0.29			0.16 0.79			AS
70	<i>Cydnius aterrimus</i> (Foster, 1771)			0.83 1.48	0.16 0.25					Ad
71	<i>Legnotus limbosus</i> (Geoffroy, 1785)	16.50 44.13	15.75 51.64	5.50 9.82	0.83 1.30	1.00 9.77	1.16 5.69	2.33 8.06	4.50 18.56	BC
72	<i>Legnotus picipes</i> (Fallén, 1807)		0.25 0.82							Ad
73	<i>Canthophorus dubius</i> (Scopoli, 1763)		0.25 0.82							Ad
*74	<i>Tritomegas bicolor</i> (Linnaeus, 1758)		1.25 4.10	0.16 0.29						Ad
*75	<i>Odontescelus fuliginosa</i> (Linnaeus, 1761)		1.25 4.10							Ad
76	<i>Odontotarsus purpureolineatus</i> (Rossi, 1790)		0.25 0.82							Ad
*77	<i>Eurygaster maura</i> (Linnaeus, 1758)		0.50 1.64	0.16 0.29	0.16 0.25	0.50 4.88	0.33 1.62	0.16 0.55		C
*78	<i>Eurygaster testudinaria</i> (Geoffroy, 1785)			0.16 0.29			0.50 2.45		0.25 1.03	AS
79	<i>Vipianus galii</i> (Wolff, 1802)		0.50 1.64							Ad
*80	<i>Graphosoma lineatum</i> (Linnaeus, 1758)	0.16 0.43		0.16 0.29				0.83 2.87		AS

Tab. 1. Continued

Nr. Taxon / Study area	1	2	3	4	5	6	7	8	Co
81 <i>Podops inuncia</i> (Fabricius, 1775)		0.25 0.82	0.16 0.29	0.16 0.25					AS
*82 <i>Sciocoris cursitans cursitans</i> (Fabricius, 1775)	1.50 4.01	0.25 0.82		0.33 0.52		0.33 1.62			AS
83 <i>Sciocoris homalonotus</i> (Fieber, 1851)	0.50 1.34								Ad
84 <i>Dryoderes umbraculatus</i> Fabricius, 1775	0.16 0.43	0.25 0.82						0.25 1.03	A
*85 <i>Aelia acuminata</i> (Linnaeus, 1775)	1.00 2.67	1.00 3.28	0.16 0.29				0.83 2.87	0.50 2.06	C
86 <i>Carpocoris purpureipennis</i> (De Geer, 1773)	0.16 0.43								Ad
87 <i>Holcostethus vernalis</i> (Wolff, 1804)	0.50 1.34								Ad
88 <i>Eurydema oleraceum</i> (Linnaeus, 1758)	0.50 1.34		0.33 0.59			0.16 0.79			AS
Nr. of species	36	33	32	35	18	25	21	14	
species diversity	2.41	2.32	1.88	2.12	2.49	2.43	2.18	1.96	
evenness	0.67	0.65	0.53	0.59	0.83	0.74	0.70	0.71	
mean abundance per sample [$A.m^{-2}$]	6.23	7.63	9.33	10.63	1.70	3.40	4.82	6.06	

A list of all collected species along with the values of their mean abundance, dominance and constancy is shown in Table 1. It was shown that in the respective study areas there were certain differences both in qualitative and quantitative structure of the investigated taxocoenoses.

The analysis of rate of similarity of qualitative structure of the respective coenoses revealed 2 clusters. The first cluster is constituted by coenoses in SAs 1, 2, and 4, and the second cluster in SAs

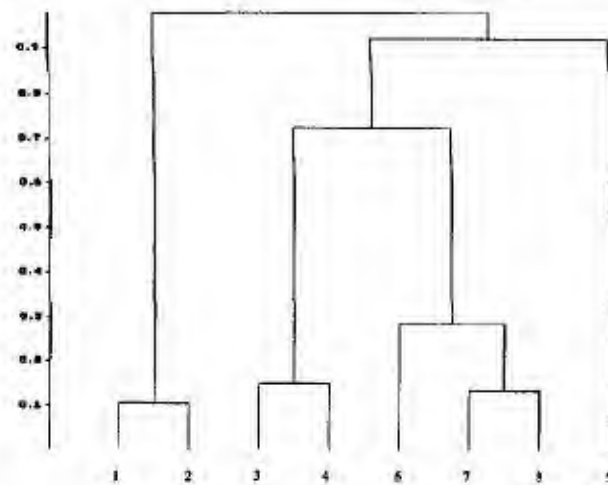


Fig. 3. Result of the eight coenoses of Heteroptera classification based on the mean annual abundance of taxa (Complete linkage clustering method, Wishart's index of similarity; numbers of study areas according to Tab. 1; vertical axis = dissimilarity level).

3, 5, 6, 7 and 8 (Fig. 2). The dendrogram shows that the differences in qualitative structure of the taxocoenoses of epigaeic Heteroptera are not sufficiently significant, this being due to the high heterogeneity of coenoses in the respective study areas. This was also confirmed by data on constancy of the individual species, from which it follows that of the total number of 84 species only 6 species were constant and 4 species were euconstant. All the other species represent only accessory and accidental elements.

Much more marked differences were found by the analysis of rate of similarity of the quantitative structure of the respective taxocoenoses (Fig. 3). First of all, a high degree of mutual similarity was seen in study areas 1 and 2 that are situated in the driest variant of floodplain forest, and, at the same time, they significantly differ from the other taxocoenoses. Particularly different from all the other coenoses was that in SA 5 characterised by a very low mean value of abundance of only 1.70 ex/m² (Table 1). A relatively high degree of similarity of quantitative representation of bugs was found in SAs 3 and 4 where the mean abundance reached the highest values (9.33 and 10.63 ex/m², respectively).

In our previous studies (Štepanovičová 1995, 1997) we reported that in floodplain forest of the Danube region 11 bug species were found, which, from the aspect of fidelity, may be designed as coenophilous species characteristic of the floodplain forest epigaeon. In our present study we determined 5 such species, and, besides their ecological characteristics (hygrophilous and mesohygrophilous species), also the relatively high values of their abundance, dominance and constancy were taken into consideration. These species are *Scolopostethus affinis*, *S. thomsoni*, *Drymus brunneus*, *D. ryell* and *Legnotus limbosus*. The significance of these species resides first of all in their high quantitative occurrence (1,028 individuals), which represents almost 68% of all individuals. It was shown that the abundance of these 5 species determines not only the quantitative conditions in the respective coenoses, but also their mutual structural similarity (Figs 3 and 4).

The qualitative and quantitative structure of taxocoenoses of the epigaeic Heteroptera may be characterized also by the species diversity (H') and evenness (e). The values of these coenologic

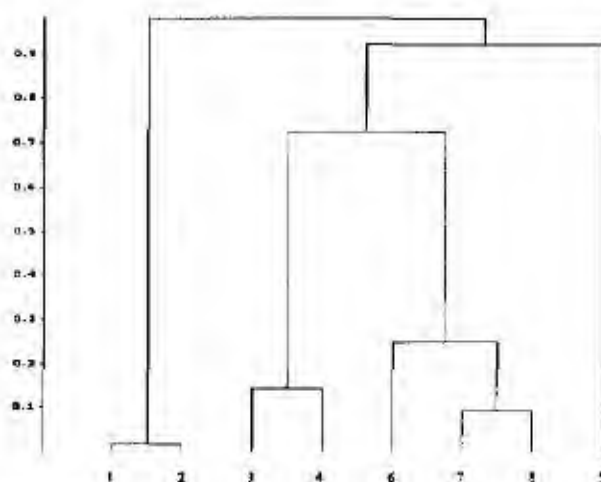


Fig. 4. Result of the eight coenoses of Heteroptera classification based on the mean annual abundance of characteristic species (Complete linkage clustering method, Wishart's index of similarity; numbers of study areas according to Tab. 1; vertical axis = dissimilarity level).

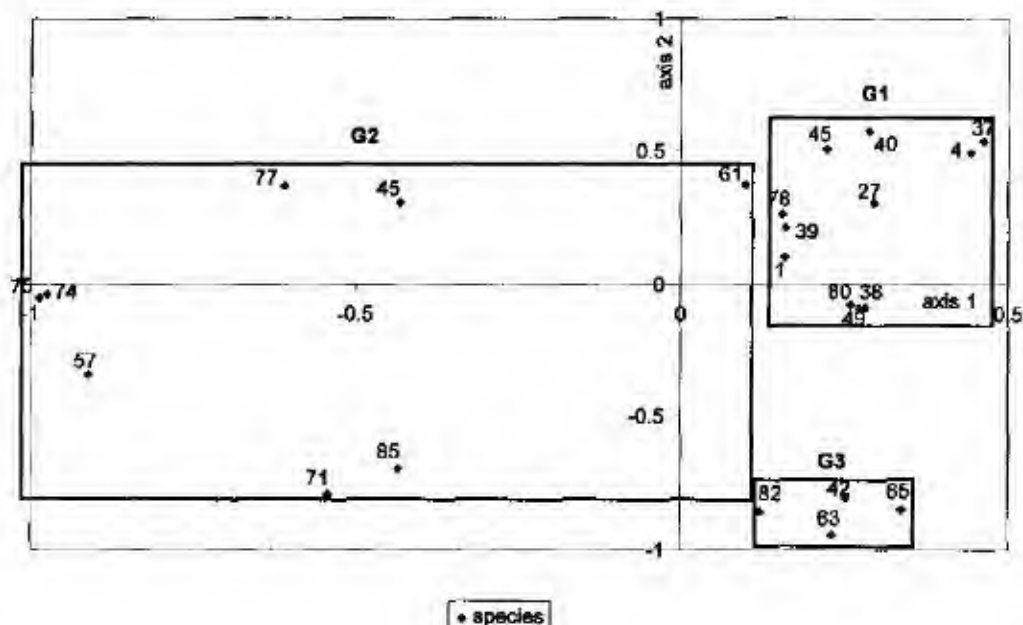


Fig. 5. PCA ordination diagram of Heteroptera taxa (selected species displayed only: species numbers according to Tab. 1).

characteristics are low (H' : 1.881–2.491, e : 0.529–0.831) and within the respective taxocoenoses they are influenced by dominance of species. The highest evenness and diversity was seen in SA 5 where the mean abundance reached the lowest value ($1.70 \text{ ex} \cdot \text{m}^{-2}$), but in this coenosis, as compared to that of the other coenoses, the range of the highest and the lowest value of dominance was the least (Tab. 1).

For the assessment of effect of some environmental factors on the occurrence of individual bug species by the PCA method 18 species were selected which at least in one of the studied areas were at least subdominant (Fig. 5). In the majority of cases these are species whose ecological requirements correspond to the conditions of the floodplain forest, or species that in the respective SA showed a more regular occurrence.

The result of PCA showed that these species constitute three separate groups which contain species with similar ecological characteristics (Fig. 5). The first ordination axis explains 25 % and the second one 24 % of variability. The first group (G 1), concentrated in the right part of axis 1, is represented by hygrophilous species whose populations occur in rather moist habitats of the floodplain forest. These are first of all 4 characteristic species, *Scolopostethus affinis*, *S. thomsoni*, *Drymus brunneus* and *D. ryell*, but also further hygrophils, such as *Ceratocombus coleoptratus*, *Holcocranum saturejae* and *Eurygaster testudinaria*. The second group (G 2) that is situated in the negative part of axis 1, is represented by species which show affinity towards drier habitats. To this group also belongs the characteristic euryhygric species *Legnotus limbosus*, some euryoecious species such as *Megalonotus chiragra*, *Eurygaster maura*, *Aelia acuminata* and *Tritomegas bicolor*, but also the xerothermophilous species *Odontoscelis fuliginosa* and *Trapezonotus*

arenarius. From these data it follows that the first PCA axis expresses the gradient of environmental moisture that in floodplain forests is a factor determining the occurrence of species which are characteristic of this type of habitat and indicate a sufficient degree of moisture. The third group (G 3) is represented by species whose populations prefer habitats with a sandy substrate. These are e. g. *Arenocoris falleni*, *Sciocoris cursitans* and *Eremocoris podagricus*.

A detailed study of effect of factors on the occurrence of the respective bug species by the CCA method showed that of the 9 tested factors, for the formation of structure of taxocoenoses of epigeic Heteroptera only 4 gradient variables play a role (moisture of soil and leaf litter – its P-value of unrestricted permutations under null model is 0.001, soil pH – $P = 0.004$, CaCO_3 content in soil – $P = 0.010$, and mean air temperature – $P = 0.006$) and two categories of one nominal variable, which are the first and the last year of investigation (1991 – $P = 0.001$ and 1996 – $P = 0.001$, respectively) (Fig. 6). These environmental variables and categories explain only 8 % of variability while final P-value of Monte Carlo permutation test is 0.001.

It was confirmed also by this method that the leading factor that most significantly influences the occurrence of bugs in floodplain forest epigaeon is the moisture of soil and leaf litter. The closest affinity to this factor was observed in *Scolopostethus affinis*, *S. pilosus*, *S. thomsoni*, *Drymus brunneus*, *Holoceranum saturejae* and *Eurygaster testudinaria*. Soil pH had the most significant effect on the species *Megalonotus chiragra*, and an increased CaCO_3 content in soil is required e.g. by the species *Raglitus alboacuminatus* and *Eremocoris podagricus*. As to the nominal variable, i. e. the years 1991 and 1996, in the analysed samples the following species occurred only in these two years: in 1991 *Trapezonotus arenarius*, *Emblethis verbasci*, *Arenocoris falleni* and *Sciocoris cursitans*, while in 1996 *Tritomegas bicolor*.

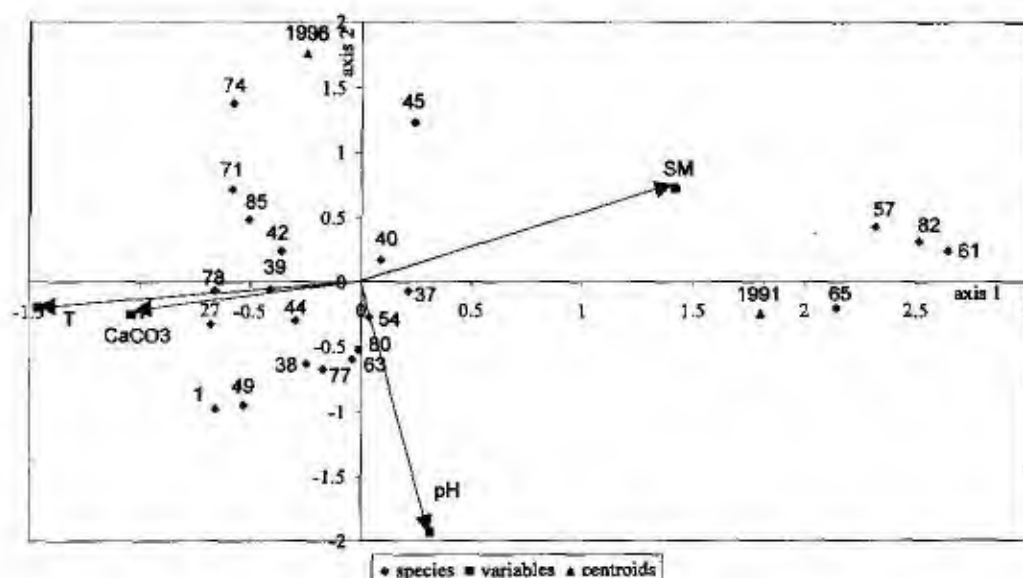


Fig. 6. CCA diagram of Heteroptera taxa (selected species displayed only) with respect to four quantitative environmental variables and one nominal variable of which classes are shown by its centroids (species numbers according to Tab. 1; SM = soil moisture, pH = soil pH, CaCO_3 = CaCO_3 content in soil, T = mean air temperature).

DISCUSSION AND CONCLUSION

Floodplain forests with their specific pedological, vegetation and ecoclimatic conditions represent an environment which offer suitable conditions of existence mainly to populations of stenoeccious, first of all hygrophilous or mesohygrophilous species of Heteroptera. This is in particular true for the floodplain forest epigaeon in which the moisture conditions are a dominant factor affecting both the qualitative and quantitative structure of bug taxocoenoses. Therefore, it appears to be a few number of species there. Krístek & Dobšík (1985) who investigated the occurrence of Heteroptera in all strata of the floodplain forest along the Dyje river in Moravia (Czech Republic), recorded the occurrence of 83 species of which only 18 species occurred on soil surface and in leaf litter. The highest quantitative representation was seen in *Drymus brunneus* and *Scolopostethus thomsoni* that occurred regularly and constituted the characteristic species also in floodplain forests of the Danube region. In floodplain forests of the Morava river in 8 study areas 23 epigaic bug species were found, of which the highest values of dominance and mean abundance were seen in the hygrophilous species *Drymus brunneus*, *Drymus ryei*, and in drier floodplain forests, in associations Fraxino-Ulmum (Tx. 1952) Oberd. 1953, also in the mesohygrophil *Legnotus limbosus* (Štepanovičová, 1994). In floodplain forests of the Danube region the populations of the latter species occurred abundantly only in SAs 1 and 2, i. e. in the driest type of this floodplain forest. The relationships of *Drymus brunneus* and *Legnotus limbosus* are discussed in a separate study in which we classify these two species as indicators of different moisture conditions in floodplain forests (Štepanovičová 1997).

In contrast to the relatively low qualitative representation of bugs in floodplain forest epigaeon of the rivers Dyje and Morava, in floodplain forests of the Danube region as many as 84 species were recorded. However it should be stressed that also here the number of coenophilous, hygrophilous and mesohygrophilous species was considerably lower and in taxocoenoses of epigaic Heteroptera in the respective study areas prevailed species that from the aspect of habitat preference of conditions of floodplain forest may be designed as xenocoenous elements.

The reasons of this situation reside in the action of the whole complex of natural (both endogenous and exogenous) and anthropogenic factors that act on the individual components of the floodplain forest ecosystem, they interact and often act synergically. First of all it should be mentioned that in the area of interest vast technical and water service activities had been carried out over the last two decades that had negatively affected whole complexes of forest communities. From the aspect of our research a marked effect was seen first of all in the decrease of groundwater level following the filling of the diversion channel and after diverting the stream from the main riverbed of the Danube. In the study areas 3 and 4, that were moreover negatively affected also by construction works, this situation resulted in a gradual aridisation and subsequent ruderalisation of floodplain forests. Subsequently, mesophilous as well as xerophilous bug species began to penetrate in the floodplain forest that occurred in the surrounding meadow, field and ruderal communities. Among these species belong e. g. *Lygus rugulipennis*, *Adelphocoris seticornis*, *Platyplax salviae*, *Metopoplax origani*, *Oxycarenus pallens*, and several others.

The penetration of xenocoenous elements was recorded also in SAs 1 and 2 characterised as the driest variant of floodplain forest, and in their vicinity to xerothermic plant community *Asparago-Crataegetum*, from which several xerothermophilous and psammophilous species of Heteroptera penetrate into the floodplain forest and occur here mainly in the vernal and autumnal aspect, in connection with hibernation. Only this can explain the occurrence of such species as e. g. *Alloeorhynchus flavipes*, *Coptosoma scutellatum*, *Thyreocoris scarabaeoides*, *Odontoscelis fuliginosa*, *Odontotarsus purpureolineatus*, *Vilpianus galii*, *Sciocoris homalonotus* and *Dyrodereus umbraculatus* in leaf litter of the floodplain forest. Their occurrence in the neighbouring forest-steppe

community *Asparago-Crataegetum* were confirmed also by our investigation in the previous years (Štepanovičová & Lapková 1984).

It may be assumed that, besides exogenous factors, the taxocoenoses of epigaeic Heteroptera in floodplain forests, their qualitative as well as quantitative structure, were determined also by endogenous factors, mainly by the fluctuating cycles in populations of dominant species, but also by the character of their dispersion, strategies of survival in times of superficial inundations, by migrations, etc.

To conclude, it may be stated that despite a number of negative effects seen first of all in 1993, when a marked decrease in the values of mean abundance of the characteristic species was recorded (Štepanovičová 1995), this situation was not irreversible and in the epigaeon of the floodplain forest the populations of five characteristic species (Tab. 1) still constitute the dominant component of taxocoenoses of Heteroptera. To this situation contribute also a number of measures taken with the aim to save the floodplain forests along the Danube, mainly by carrying out simulated inundations and by filling water into the arm system of the Danube.

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Morphological variation and polyvoltinism of *Microvelia pulchella* (Heteroptera: Veliidae) in southern Illinois, USA

Steven J. TAYLOR¹⁾ & John E. MCPHERSON²⁾

¹⁾ Center for Biodiversity, Illinois Natural History Survey, 607 East Peabody Drive, Champaign, Illinois 61820 USA

²⁾ Department of Zoology, Southern Illinois University at Carbondale, Carbondale, Illinois 62901-6501 USA

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Abstract. Voltinism in *Microvelia pulchella* Westwood, 1834 was studied in southern Illinois during 1989 and 1990. This species overwintered as eggs, which hatched during April. First instars were found from mid-April through mid-October, second instars from mid-April through mid-October, third instars from late April through late October, fourth instars from late April through mid-November, and adults from early May through early November. The sequences of peaks of nymphal instars and adults indicated that this species had 4–5 generations per year. *M. pulchella* was reared from egg to adult at 23.3±1.1 °C under a 14L:10D photoperiod. The incubation period averaged 9.85 days; and the first through fourth stadia averaged 8.18, 6.14, 6.32, and 7.72 days, respectively. Total developmental time averaged 34.07 days.

Life history, voltinism, morphological variation, Heteroptera, *Microvelia pulchella*, Illinois

INTRODUCTION

Microvelia pulchella Westwood, 1834 occurs from Newfoundland, Nova Scotia, New Brunswick (Scudder 1987), Quebec, New York, and Massachusetts south to Florida and west to British Columbia and California (Smith 1988); it also has been recorded from the West Indies and from Mexico into South America (Smith 1988). It occurs throughout much of Illinois (Taylor 1996).

Much of the life history and other biological data for *M. pulchella* has been published under various synonyms (Smith 1988), two of the most frequently encountered being *Microvelia borealis* Torre-Bueno, 1916 and *Microvelia capitata* Guérin-Ménéville, 1857 (Drake & Hussey 1955, Polhemus & Chapman 1979, Smith 1988, Smith & Polhemus 1978). The summary of these biological data below, therefore, includes information associated with these three names.

Microvelia pulchella has been collected from ponds, lakes, and cypress swamps in North and South Carolina (Sanderson 1982); pond and river habitats in Virginia (Bobb 1974); lentic habitats throughout Wisconsin (Hilsenhoff 1986); lakes, ponds, marshes, rivers, and creeks, especially in association with *Typha*, *Carex*, and *Lemna*, in Minnesota (Bennett & Cook 1981); a pond with much calcareous sediment and many water weeds in Indiana (Blatchley 1926); ponds and lakes in Illinois (Taylor 1996); ponds in California (Polhemus & Chapman 1979); permanent ponds in Missouri (Froeschner 1962); lake, pond, and stream habitats in New Jersey (Chapman 1959); sinkholes, calcareous streams, roadside ditches, *Nymphaea* marshes, sand-bottomed creeks, and fluctuating hammock region ponds in northern Florida (Herring 1950); ponds and a creek, all of which were mud-bottomed and associated with abundant vegetation, in southeastern Louisiana (Ellis 1952); quiet streams, ponds, and sloughs in Mississippi (Wilson 1958); and fens and marshes in Canada (Scudder 1987). It has been found with *Microvelia americana* (Uhler, 1884) and *Microvelia hinei* Drake, 1920 in Virginia (Bobb 1974); *Gerris marginatus* Say, 1832, *Limnoporus canaliculatus* (Say,

1832), *Neogerris hesione* (Kirkaldy, 1902), *Rheumatobates palosi* Blatchley, 1926, *Trepobates subnitidus* Esaki, 1926, *Merragata brunnea* Drake, 1917, *Merragata hebroides* White, 1877, *Hydrometra martini* Kirkaldy, 1900, *Mesovelvia cryptophila* Hungerford, 1924, *M. mulsanti* White, 1879, *Microvelia hinei* Drake, 1920, and *Steinovelvia stagnalis* (Burmeister, 1835) in southern Illinois (Taylor 1996); and *Microvelia buenoi* Drake, 1920, *Limnoporus notabilis* (Drake et Hottes, 1925), and *Mesovelvia mulsanti* in Canada (Scudder 1987).

Torre-Bueno (1917) and Bobb (1974) reported that *M. pulchella* overwinters as adults; however, Hilsenhoff (1986) noted that, in Wisconsin, adults had not been collected before June, suggesting that this species overwinters as eggs. It apparently is multivoltine (Hilsenhoff 1986, Torre-Bueno 1917). Eggs are laid on the undersurface of duckweed, or on other substrates, in a clear waterproof glue (Torre-Bueno 1917). Hungerford (1920) also reported on the life history of *M. pulchella*; however, because of his apparent misidentification of this species (see below), we have chosen not to include his information.

Microvelia pulchella has been collected in September and October in Missouri (Froeschner 1962); August, September, and October in New Jersey (Chapman 1959); January, November, and December in Louisiana (Ellis 1952); June, July, August, August-September, and November in Mississippi (Wilson 1958); and most months of the year in northern Florida (Herring 1950). Both macropterous and apterous forms are known, but most adults are apterous. For example, macropterous individuals represented only 2.7% of the 1,499 adults examined in Wisconsin (Hilsenhoff 1986) and 5.7% of the 384 adults examined in Illinois (Taylor 1996). Bobb (1974) found only apterous adults in Virginia.

The difficulty in distinguishing *M. pulchella* from other species, and in differentiating instars within this species, has affected the reliability of earlier studies. One result has been confusion regarding the number of instars in this species.

Torre-Bueno (1917) and Hoffmann (1925) (also spelled Hoffman, see Polhemus & Polhemus 1988: 537) reared nymphs through four stadia to adults. Hungerford (1920) stated that he had found "more than this in some." However, Hungerford's samples may have contained specimens of *Microvelia hinei*, a possibility suggested by Bobb (1974) and Hoffmann (1925) and further supported by the fact that these species have been collected together in the same field samples in Illinois (Taylor 1996) and Virginia (Bobb 1974). Frick (1949), working with a Panama population of *M. pulchella*, also stated he reared nymphs through four and five stadia to adults. However, as suggested for Hungerford's (1920) results, Frick's samples may have contained mixed species. All adults reared by Hoffmann (1925) were apterous, but he felt that macropterous adults also would have only four instars.

Most Heteroptera have five instars, with fewer instars or a variable number being uncommon (Štys & Davidová-Vilímová 1989). Within *Microvelia* Westwood, 1834, species other than *M. pulchella* have five instars (e. g., *M. diluta* Distant, 1909 [Miyamoto 1953], *M. hinei* [Hoffmann 1925], *M. albonotata* Champion, 1898 [Hoffmann 1925], *M. americana* [Uhler] [Torre-Bueno 1910]) or four (e. g., *M. macgregori* Kirkaldy, 1899 [Don 1967], *M. buenoi* [Hoffmann 1925]), but none, other than *M. pulchella*, has been reported to have a variable number (Štys & Davidová-Vilímová 1989). So, either *M. pulchella* is unusual in having a variable number of instars or, perhaps, the reported variation has resulted from taxonomic problems (i. e., mixed species in samples). Yet another explanation for these discrepancies is the possible misinterpretation of marked size variation in this species (e. g., Drake & Hussey 1955, Kirby 1890), which would make it difficult to distinguish instars on the basis of general body size.

Torre-Bueno (1917) reared *M. pulchella* under uncontrolled conditions. The incubation period was 7–23 days; the first through fourth stadia, 2–11, 2–6, 3–6, and 4–10 days, respectively; and total development from egg to adult, 22–59 days.

Presented here is information on voltinism in *M. pulchella*, including times of occurrence of the nymphal instars and adults. We also discuss our method for distinguishing instars in field populations and, as confirmation, present the results of our rearing of this insect under controlled photoperiod and temperature conditions.

MATERIAL AND METHODS

Field life history studies

During 1989 and 1990, we studied voltinism in a population of *M. pulchella* at President's Pond on the Southern Illinois University at Carbondale campus, Jackson County, Illinois (see Taylor [1996] for detailed description of pond). This pond is roughly triangular, 0.29 hectare (0.71 acre) in surface area, and connected at the northern end to an adjacent lake by a narrow channel (approximately 2–5 m wide, 2 m deep). Along the eastern shore (where the present study was conducted), water depth increased sharply between 1 and 2 m from shore and commonly exceeded 2 m at 2.5 m from shore.

Floating, emergent, and shoreline vegetation associated with the pond was diverse (Taylor 1996). The western margin was bordered by a narrow, dense band of cattails (*Typha angustifolia* L.). The southern border was comprised of a riprap dam covered with soil and crossed by a paved road. The eastern margin was bordered by overhanging trees and other vegetation. During the summer, the pond filled with a dense growth of aquatic vascular plants and filamentous algae. Near the shoreline, and wherever the aquatic plants reached the water surface, duckweeds built up into dense mats. The duckweeds (i.e., *Lemna minor* L., *Spirodela polyrrhiza* (L.) Schleiden, and *Wolffia papulifera* Thompson) tended to move around the pond because of air currents unless the plants were anchored in the underlying aquatic vegetation.

Samples were collected weekly from 18 March to 25 November 1989, and biweekly from 11 February to 2 December 1990. Sampling was confined to an area along the eastern shore because (1) the cattails along the western shoreline prevented use of the quadrat sampler (see below), (2) the riprap shoreline of the southern border was unnatural and often disturbed by fishermen, and (3) the water surface along the eastern shore, which was a mosaic of open water, duckweeds, and emergent stems, supported a diverse gerrhonormorph fauna.

Four 60 m transects were made parallel to a relatively uniform section of the eastern margin at 0, 0.5, 1.0, and 1.5 m from the shoreline. Each sample was collected with a floating quadrat sampler (0.25 × 0.25 × 0.05 m), with four replicates placed randomly along each transect; the resulting 16 quadrat samples were pooled, providing a broad sampling of the habitat. Prior to each sample, the collector (SJT) stood for approximately three minutes to allow the insects to acclimate to the disturbance; then, the sampler was placed on the surface of the water. Specimens were removed with a fine mesh nylon net, preserved in alcohol, and sorted in the laboratory.

Adults could be distinguished from nymphs by the full development of external genitalia and degree of sclerotization. However, distinguishing nymphal instars was difficult because of size variation, the presence of both apterous and macropterous adults, and the possibility of both four and five instars (see discussion above). Nymphal instars of other gerrhonormorph species have been separated by the lengths of leg segments (Galbraith & Fernando 1977, Kittle & McCraw 1981, Matsuda 1960, 1961a, b, Vepsäläinen & Järvinen 1974), and the use of morphometrics to separate instars is used widely in a variety of insect groups (Daly 1985). Therefore, we first measured the lengths of the meso- and metafemora and tibiae and length of the body in field-collected adults to determine if these measurements reflected variation in body size. If so, we hoped that one of these leg segments could be measured in nymphs to determine the number of instars. The adults used for these measurements were collected with a D-net on 3 September 1990 from a population at Bean Ridge Pond, Alexander County, Illinois.

Laboratory Rearing

Thirty apterous adults were collected with a D-net at President's Pond on 4 November 1990, brought to the laboratory, and placed in plastic containers (5 males, 5 females / container). Each container (3.5 cm deep × 5.4 cm diam. [top] and 3.7 cm diam. [bottom]) was half filled with deionized water. A plastic disk (3.5 cm diam.), with 7 holes (each 0.6 cm diam.) was placed on the surface; the holes were made to create a longer intersection line (Hess & Hall 1943) between the "land" (plastic disk) and water. Two paper strips of cardstock (approximately 1.25 × 2.5 cm) were angled against opposite sides of each container with the tops above the water. The disks and strips served as oviposition sites and allowed individuals to leave the water.

Containers were checked daily for eggs. Disks or paper strips with attached eggs were placed in new containers. If eggs were deposited on the walls of the container, adults were moved to a new container. As eggs hatched, the newly emerged first instars were placed in new containers prepared similarly to those for adults but without paper strips. Nymphs of the same instar molting into the subsequent instar on the same day were moved to new containers if other nymphs in the container had not molted.

Tab. 1. Body measurements (mm) of adult *Microvelia pulchella* Westwood collected 3 September 1990 from Bean Ridge Pond

Measurement (Length)	N	Sex	Mean \pm Std. Err.	Range
Body ^a	46 ^b	male	1.63 \pm 0.02	1.32-1.92
	120 ^b	female	1.53 \pm 0.01	1.39-1.79
Mesofemur	125	male	0.37 \pm 0.01	0.37-0.64
	124	female	0.43 \pm 0.00	0.39-0.48
Mesotibia	125	male	0.39 \pm 0.00	0.26-0.49
	124	female	0.38 \pm 0.00	0.35-0.45
Metafemur	124	male	0.54 \pm 0.01	0.41-0.71
	124	female	0.45 \pm 0.00	0.39-0.51
Metatibia	124	male	0.58 \pm 0.01	0.47-0.73
	124	female	0.55 \pm 0.00	0.50-0.61

^a Longitudinal measurements were taken along midline of body from front of head to posterior end of genital segments

^b N values for body length are smaller than those for other measurements because some specimens expanded in alcohol and their lengths could not be measured accurately.

The water level was maintained just above (0.1-0.3 cm) the eggs. Maximum numbers of individuals reared per container were: six first instars, four second instars, three third instars, and one fourth instar. Adults reared from these eggs were preserved in 70% ethanol.

Each adult was fed two, and each nymph one half, frozen adult fruit fly (*Drosophila melanogaster* Meigen) per day; flies were replaced daily. Flies were crushed or torn slightly for nymphs to facilitate feeding.

All individuals were maintained in incubators at 23.3 \pm 1.1° C and a 14L:10D photoperiod. All containers were changed at least once per week but more frequently when water became cloudy.

Statistical analyses

Data were analyzed with the SAS (SAS Institute 1988) TTEST procedure. Level of significance was 0.05.

RESULTS

Field life history

The population of *M. pulchella* at President's Pond was large (1,567 adults and 2,974 nymphs collected during 1989 and 1990). However, even with this large population, an understanding of voltinism was complicated by the uncertainty in number of instars (4 or 5) and the previously

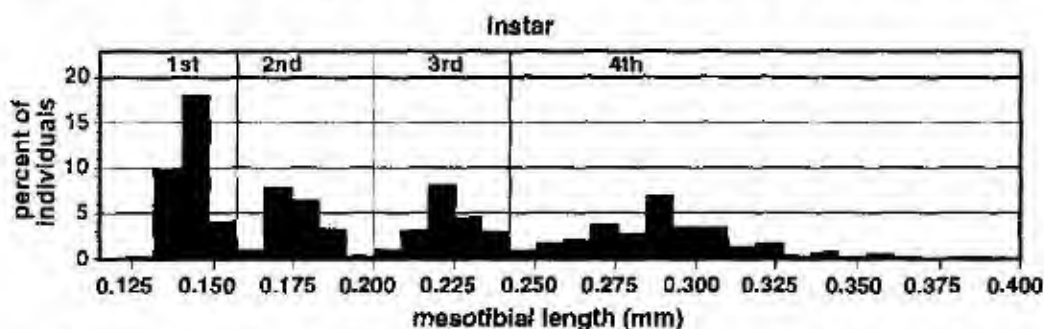


Fig. 1. Approximate instars of *Microvelia pulchella* Westwood (N=2,973) as delineated by mesotibial length (mm). Based on 1989 and 1990 collections from President's Pond.

Tab. 2. Correlations, by sex, among various body measurements of adult *Microvelia pulchella* Westwood collected 3 September 1990 from Bean Ridge Pond. For each pairwise correlation, values are Pearson Correlation Coefficient (top) and sample size (bottom). All pairwise correlations were significant ($p < 0.0001$).

Sex	Measurement (Length)	Measurement (Length)			
		Mesofemur	Mesotibia	Metafemur	Metatibia
Male	Mesotibia	0.8762 125			
	Metafemur	0.9084 125	0.9248 124		
	Metatibia	0.8481 124	0.8751 124	0.9072 124	
	Body ^a	0.8386 46	0.9338 46	0.9776 46	0.8495 46
Female	Mesotibia	0.6012 124			
	Metafemur	0.8286 124	0.5664 124		
	Metatibia	0.7748 124	0.6206 124	0.8228 124	
	Body ^b	0.7517 120	0.6345 120	0.7092 120	0.7313 120

^a Longitudinal measurements were taken along midline of body from front of head to posterior end of genital segments.

^b N values for body length are smaller than those for other measurements because some specimens expanded in alcohol and their lengths could not be measured accurately.

reported size variation. Because we needed a diagnostic character to allow separation of instars (as noted above), we measured the lengths of the meso- and metafemora and tibiae and body of adults (Table 1) and examined the correlations among these measurements (Table 2). All correlations were significant. Therefore, potentially, each of the measurements could be used to distinguish instars. We selected the mesotibiae as our diagnostic character for the following reasons: (1) bodies in Gerronomorphans tend to change in length under various conditions (e.g., Brinkhurst 1959, Matsuda 1961a, Sprague 1956), especially in nymphs, (2) femora are closer to the body, thus making them more difficult to measure, and (3) metatibiae in adult male *M. pulchella* are curved, which, potentially, could have affected correlations. Measurements of the mesotibiae in our field-collected nymphs indicated that there were four instars (Fig. 1), which was confirmed by laboratory rearing (see below). Thus, we were better able to understand voltinism in this species.

Microvelia pulchella overwintered as eggs in southern Illinois, although no eggs were collected; the first active individuals in spring were nymphs. First instars were collected from mid-April through mid-October, second instars from mid-April through mid-October, third instars from late April through late October, fourth instars from late April through mid-November, and adults from early May through early November (Figs 2-5).

Voltinism was difficult to determine because of the extreme overlap of nymphal instars and adults and the continuous or near continuous presence of these stages across seasons. However, Figs 2-3 (1989) and Figs 4-5 (1990) suggested five or four generations, respectively, with the final complete generation reaching adults in October and November. These adults, then, laid overwintering eggs.

In contrast to our results, and those of Hilsenhoff (1986) and Torre-Bueno (1917), data from Illinois museum specimens collected throughout the state suggested two generations per year.

Tab. 3. Durations (in days) of immature stages of laboratory-reared *Microvelia pulchella* Westwood

Stage	Sex	Number completing stadium	Mean \pm Std. Err.	Range
Egg*		123	9.85 \pm 0.07	9-15
First instar		107	8.18 \pm 0.16	5-13
Second instar		73	6.14 \pm 0.19	4-12
Third instar		74	6.32 \pm 0.18	4-11
Fourth instar	Males + Females	46	7.72 \pm 0.21	5-12
	Males	28	7.79 \pm 0.26	6-11
	Females	18	7.61 \pm 0.37	5-12
Egg through fourth instar	Males + Females	30	34.07 \pm 0.57	28-43
	Males	19	34.42 \pm 0.66	30-43
	Females	11	33.46 \pm 1.07	28-42

* 174 eggs were laid.

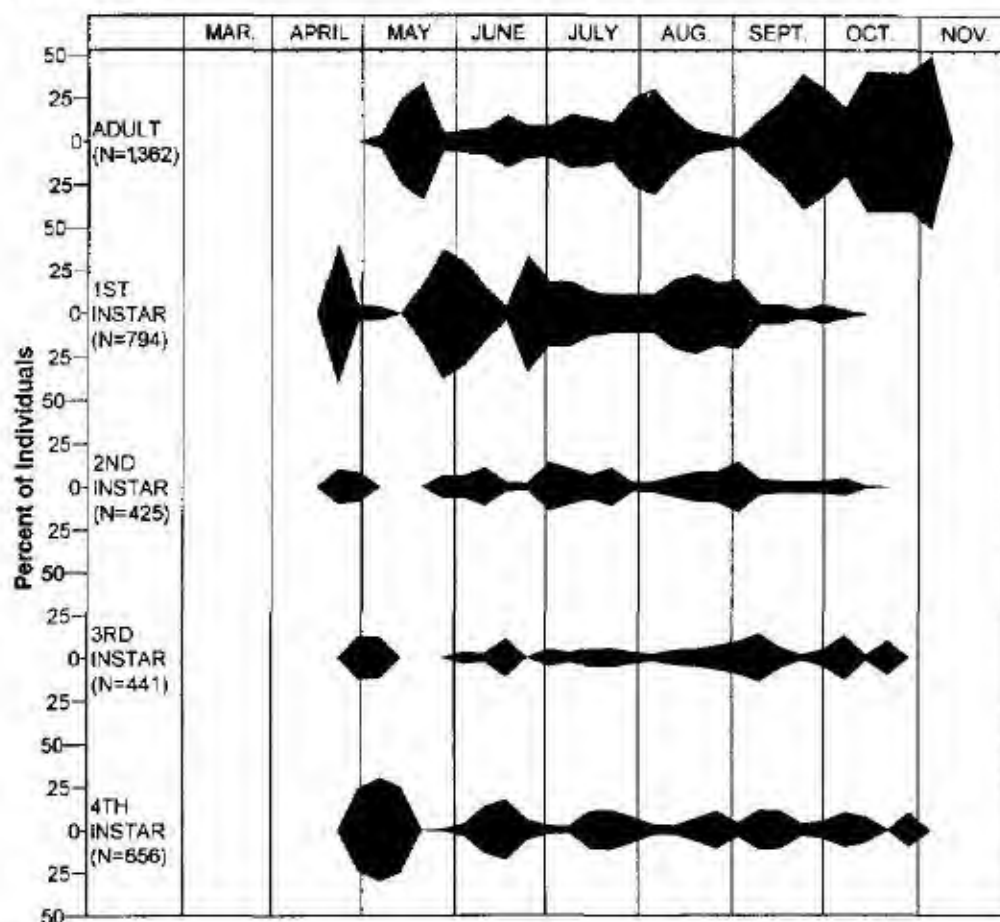


Fig. 2. Percent of individuals in each stage per sample of *Microvelia pulchella* Westwood collected during 1989 from President's Pond.

(Taylor 1996). This apparent discrepancy may be the result of the museum specimens having been collected over the entire state over a number of years, which could have masked generation peaks. Of the 1,567 adults collected at President's Pond, 797 were males and 770 were females; of these, 1,564 were apterous (796 males, 99.9%; 768 females, 99.7%) and three were macropterous. The macropterous adults were collected in July (1 female) and September (1 male, 1 female), 1989.

When male and female adult mesotibial lengths were plotted across the year (Fig. 6), it was apparent that spring and fall individuals were generally larger than summer individuals. Adult size variation in mesotibial length of both sexes appeared to be normally distributed (Fig. 7). All adult males had distinctly curved metatibiae, although curvature was less apparent in smaller individuals.

Laboratory Rearing

Eggs (N=174) were deposited on the paper strips in contact with, or near, the water (133); on the walls of the container (18); and on the underside of the floating disks (23). The incubation period

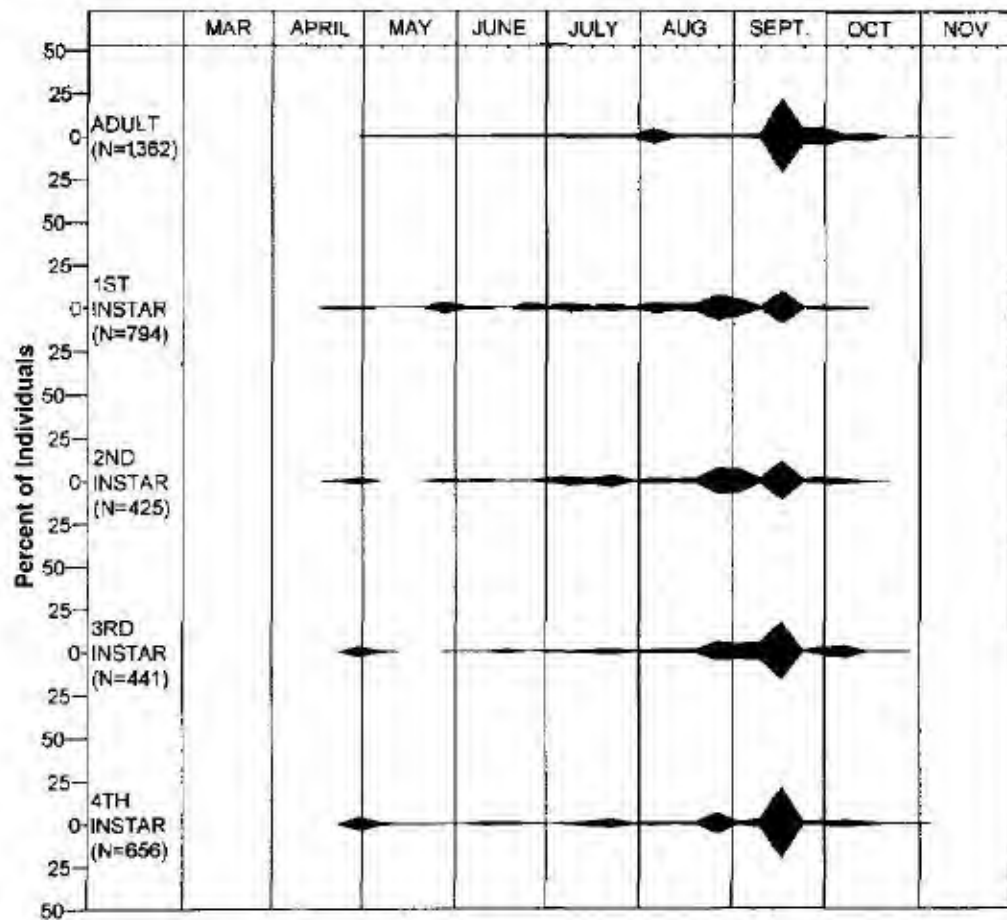


Fig. 3 Percent in each sample of total individuals of same stage of *Microvelta pulchella* Westwood collected during 1989 from President's Pond.

averaged 9.85 days (Table 3). The four subsequent stadia averaged 8.18, 6.14, 6.32, and 7.72 days, respectively. Total developmental time averaged 34.07 days. No sexual difference was detected in length of the fourth stadium ($T=0.398$, $df=44$, $p=0.693$) or in total developmental time ($T=0.814$, $df=28$, $p=0.423$).

Deaths of first instars resulted primarily from drowning during the first two days following eclosion; deaths in later instars usually resulted from incomplete ecdysis.

Thirty individuals (19 males, 11 females) were reared to adults from eggs of known age; all were apterous. Eighteen additional individuals were reared from eggs of unknown age (oviposition date not recorded during laboratory rearing); of these, 16 were apterous and two (1 male, 1 female) were macropterous. All 48 individuals passed through only four instars.

Thirteen laboratory-reared adult females were paired with males as they became adults or shortly thereafter; of these, 12 subsequently oviposited. The preovipositional period averaged 7.92 days (range 5–16). The oviposition period averaged 17.33 days (range 1–42), with a total of 138 eggs

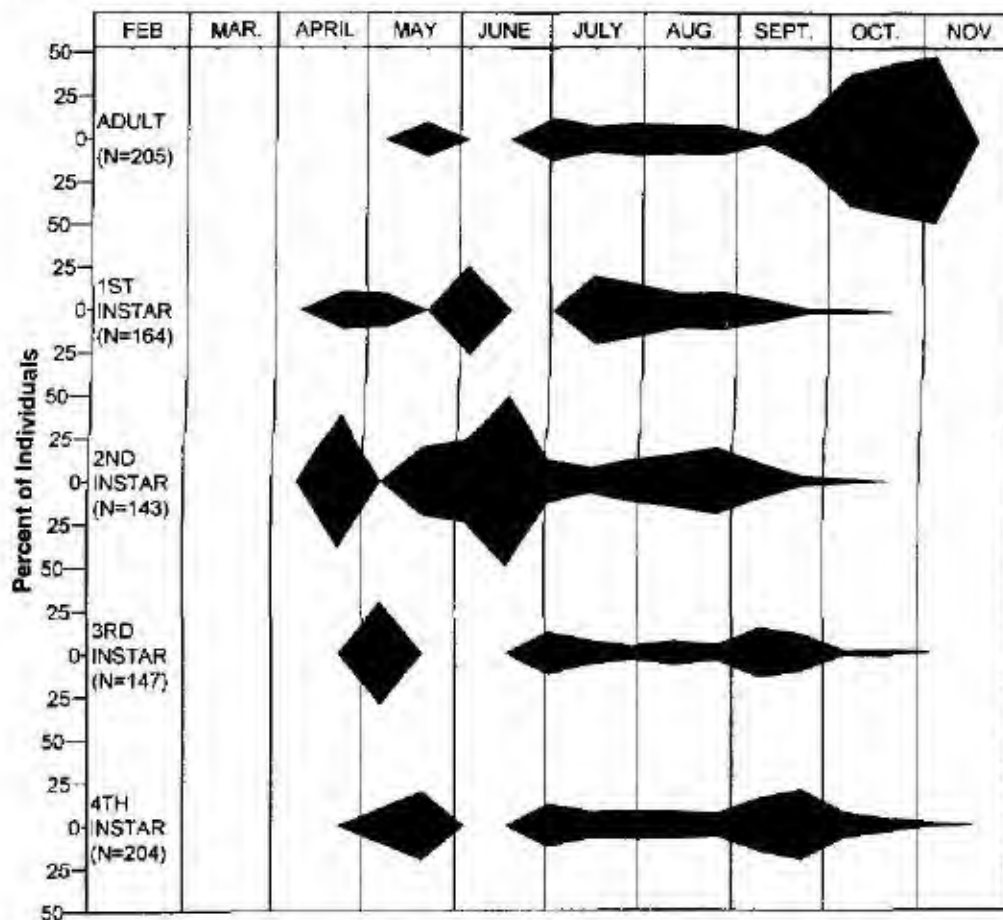


Fig. 4. Percent of individuals in each stage per sample of *Microvelia pulchella* Westwood collected during 1990 from President's Pond.

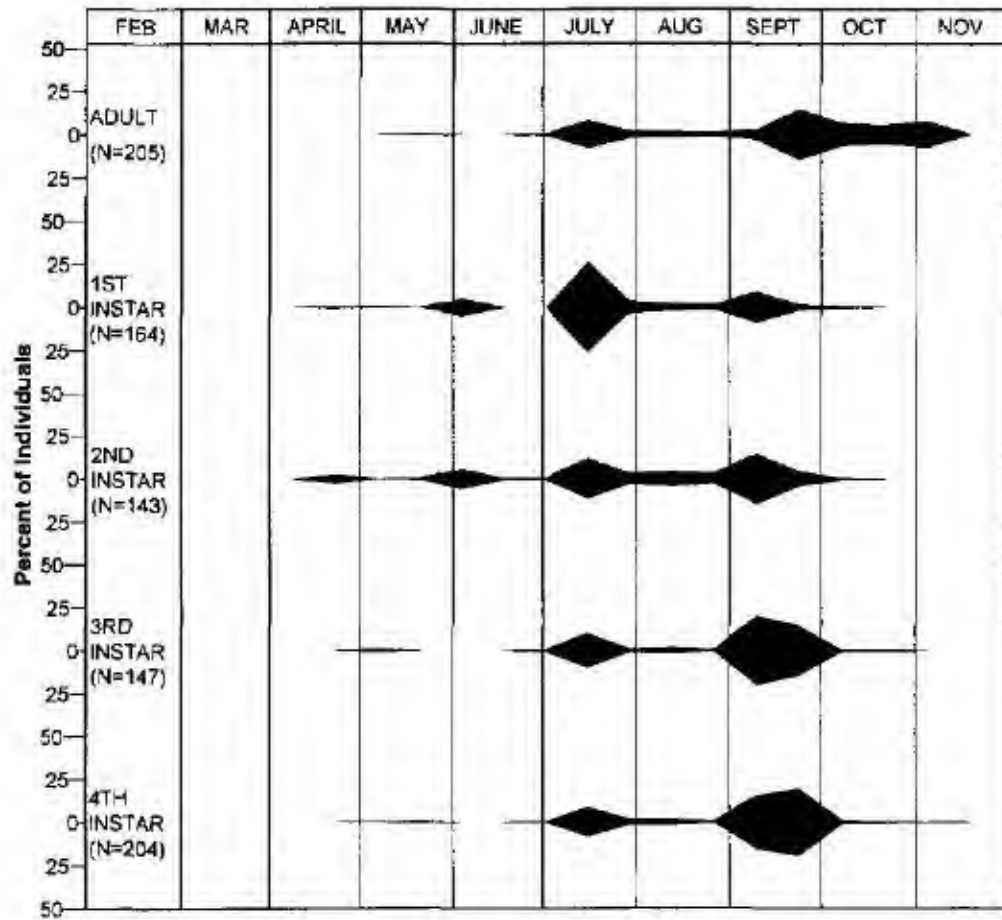


Fig. 5. Percent in each sample of total individuals of same stage of *Microvelia pulchella* Westwood collected during 1990 from President's Pond.

(range 1–41) laid. Number of eggs laid per female per day averaged 0.65 (range 0–4). One breeding male lived for 69 days, and one ovipositing female for more than 69 days, after reaching adult.

There was no sexual difference in mean mesotibial lengths (in mm) of laboratory-reared adults (males, 0.410 ± 0.005 [range, 0.387–0.468], $N=19$; females, 0.421 ± 0.004 [range, 0.403–0.444], $N=14$; $df=18, 13$, $T=-1.8061$, $p=0.0806$). Also, mesotibial lengths generally fell within the range of those for field-collected specimens of both sexes (Figs. 6 and 7, Table 1).

During laboratory rearing, we observed adult males of *M. pulchella*, usually in the presence of adult females, making leg movements that caused the posterior end of the body to go up and down several times in rapid succession.

DISCUSSION

Our laboratory-rearing data (Table 3) showed that all adults developed through four nymphal instars, thus confirming the reports of Torre-Bueno (1917) and Hoffmann (1925). The occurrence of two macropterous adults among our reared specimens also supports Hoffmann's (1925) opinion that macropterous individuals probably would have four instars. That no individuals developed through five nymphal stadia adds more doubt to Frick's (1949) report of four and five instars and Hungerford's (1920) report of primarily four instars but "more than this in some". Still, it may be that under different conditions (e. g., food, photoperiod, temperature) or in another population (e. g., Frick's Panama population), we also might have found five nymphal stadia. Our collections at President's Pond show that *M. pulchella* can exist syntopically with *M. hinei*, which has five instars

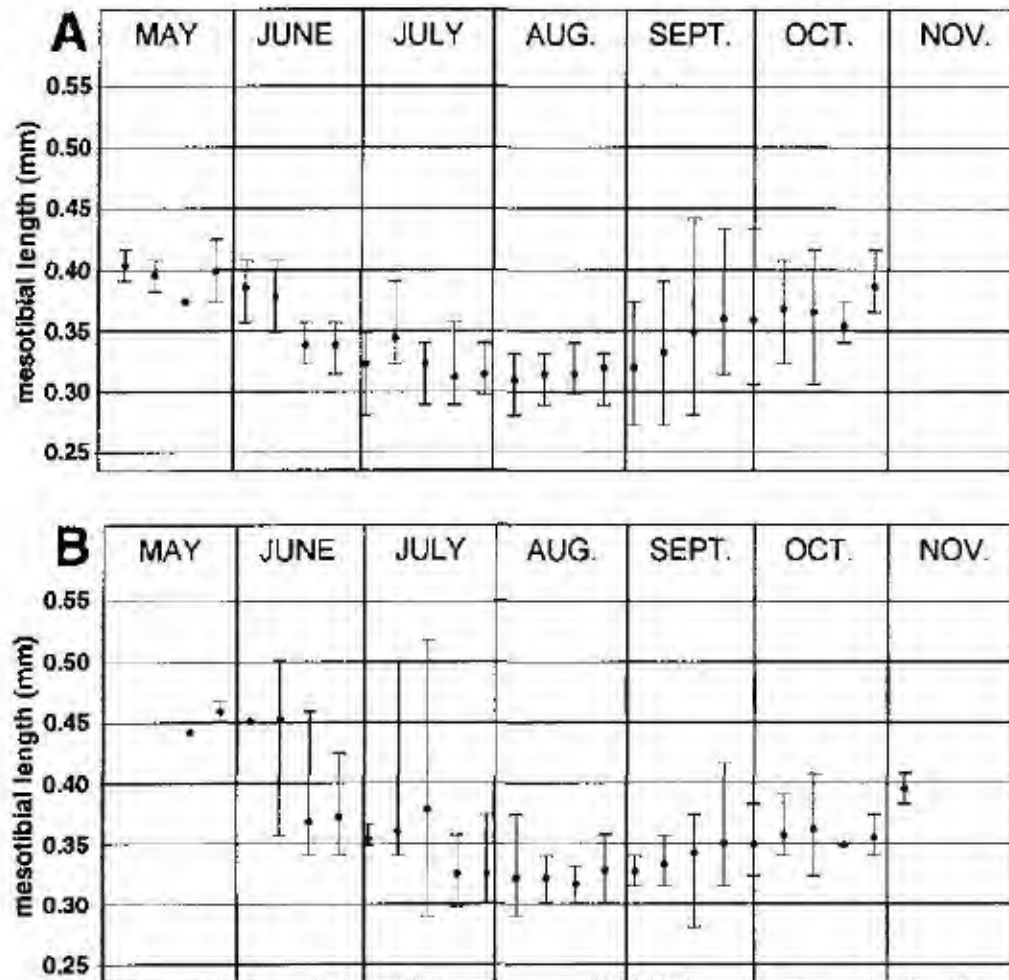


Fig. 5 Mean and range of mesotibial lengths (mm), by sample date, for *Microvelia pulchella* Westwood adults collected during 1989 from President's Pond. A, males (N=715); B, females (N=646).

and is superficially similar in appearance; this supports Hoffmann's (1925) and Bobb's (1974) opinion that Hungerford's (1920) rearing data might have been based on mixed species samples.

Our laboratory observations of vibratory behavior in *M. pulchella* are not unique within *Microvelia*. Frick (1949) also noted that males of *M. pulchella* "let out a series of spasmodic jerks up and down, lasting approximately a second." Similar behavior has been reported by Polhemus (1990) for *M. longipes* Uhler, 1894. He observed males of this species producing surface waves, noting that individuals "would vibrate for 15 to 30 seconds, then cease for a time." He suggested these movements might serve in intraspecific communication, as has been reported in the Gerridae (e. g., Spence & Andersen 1994, Wilcox 1995).

Microvelia pulchella offers many additional opportunities for study. The limited space needed for rearing (relative to the larger, yet better studied, Gerridae), ease of feeding, and the capacity of this species to pass through multiple generations per year make it well suited for laboratory studies. The impacts of a variety of parameters (e. g., predation, reproductive behavior and strategies, vibratory signals, temperature, photoperiod, nutrition, character displacement, and seasonal and geographic variation) on morphology and/or reproduction in *M. pulchella* should provide fertile ground for future research, especially in light of the strong theoretical framework already established through studies of the sister family Gerridae (e. g., Fairbairn 1997, Klingenberg & Spence 1997, Rowe et al. 1994, Spence & Andersen 1994, Wilcox 1995).

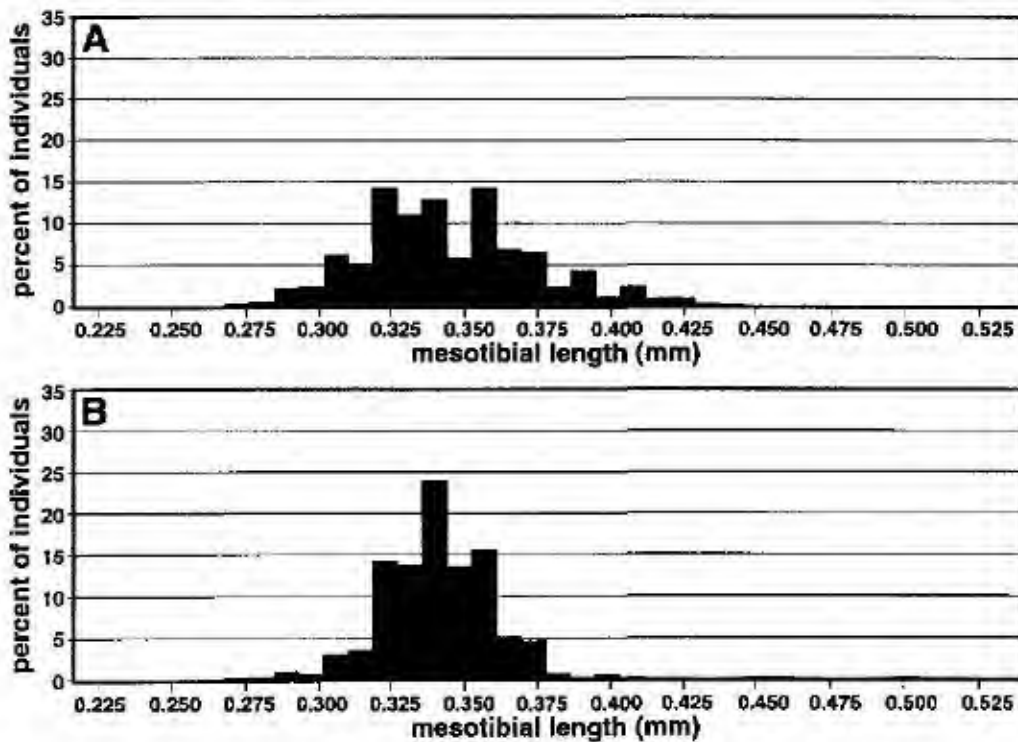


Fig. 7. Mesotibial lengths (mm) of *Microvelia pulchella* Westwood adults collected during 1989 from President's Pond. A, males (N=715); B, females (N=646).

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Notes on the genus *Distotrephes* (Heteroptera: Helotrephidae): new species from Thailand, Laos, and China, a key to species, and first description of the macropterous morph

Herbert ZETTEL

Naturhistorisches Museum in Wien, 2. Zoologische Abteilung, Burgring 7, A-1014 Wien, Austria

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Abstract. Five species of the genus *Distotrephes* Polhemus, 1990, are newly described: *Distotrephes* (s. str.) *pavelstysi* sp. n. (from Thailand: Chiang Mai, Mae Hong Son, and Laos: Luang Nam Tha), *D.* (s. str.) *schwendingeri* sp. n. (from Thailand: Phetchabun, Phrae), *D.* (s. str.) *shepardi* sp. n. (from Thailand: Phetchabun), *D.* (s. str.) *laotensis* sp. n. (from Laos: Luang Nam Tha), and *D.* (s. str.) *ju* sp. n. (from China: Hainan). New distribution data of *D.* (s. str.) *stysi* Polhemus, 1990, and *D.* (s. str.) *asymmetricus* Zettel, 1995, from China are presented. An identification key to the *Distotrephes* (s. str.) species is introduced. The macropterous morph of *Distotrephes* is described for the first time, differing from the hind-wing-macropterous morph also in larger eyes, which are not completely transected by the lateral carina of the cephalonotum.

Taxonomy, macropterous morph, eye dimorphism, new species, new records, key, Heteroptera, Helotrephidae, *Distotrephes*, Oriental region

INTRODUCTION

Species of the genus *Distotrephes* Polhemus, 1990, are small sized Helotrephidae with semi-globular appearance. In contrast to most other Limnotrephini: Polhemus, 1990 (e.g., species of the genera *Idiotrephes* Lundblad, 1933, and *Tiphotrephes* Esaki et China, 1928), who prefer stagnant waters, *Distotrephes* are found in clean brooks and streams, where they inhabit stone or gravel sediments or accumulated plant material in the currents (Zettel 1997). Five species in two subgenera are so far described, who were recently revised by the author (Zettel 1995). The subgenus *Distotrephes* (*D. stysi* Polhemus, 1990, *D. asymmetricus* Zettel, 1995) is so far known from China and Viet Nam, the subgenus *Polhemotrephes* Zettel, 1995 (*D. heveli* Polhemus, 1990, *D. sarawakensis* Zettel, 1995, *D. kodadai* Zettel, 1995) occurs in Borneo. In this paper further five species are newly described from Thailand, Laos, and China, they all belong to the subgenus *Distotrephes* s. str.

A key to the helotrephid genera occurring in Southeast Asia was recently published by Zettel (1998).

Specimens are hind-wing-brachypterous if not otherwise stated (according to the absence of a claval suture on the hemelytron).

This paper is dedicated to Prof. Dr. Pavel Štys, one of the most outstanding heteropterists of the last decades, to celebrate his 65th birthday. In several contributions he influenced the research on helotrephid morphology in a very fruitful way.

MATERIAL

Specimens are deposited in the following collections

- CASS Chinese Academy of Sciences, Institute of Applied Ecology, Shenyang, China;
CHMU Chiang Mai University, Faculty of Sciences, Department of Biology, Chiang Mai, Thailand;
CNT Coll. N. Nicser, Tiel, The Netherlands;
CPC Coll. P. P. Chen, Beijing, China;
CSS Coll. W. D. Shepard, Sacramento, USA;
JTPC Colorado Entomological Museum [= J.T. Polhemus Collection], Englewood, Colorado, USA;
KKUA Khon Kaen University, Faculty of Agriculture, Department of Entomology, Khon Kaen, Thailand;
NMW Natural History Museum Vienna, Austria.

SYSTEMATIC PART

Distotrephes Polhemus, 1990

Generic diagnoses were presented recently, first by Polhemus (1990), and later-on by Zettel (1995) for both subgenera. Due to some deviations of new species, a corrected diagnosis is given.

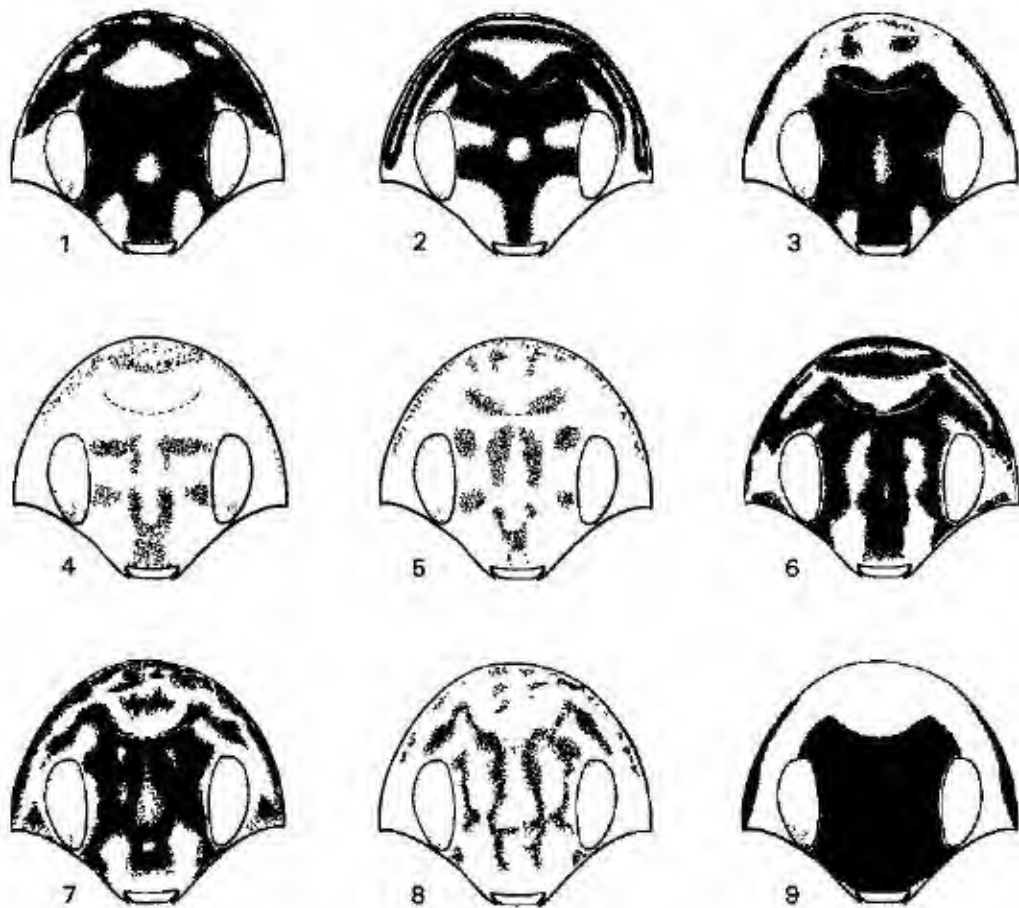
DIAGNOSIS. small, semi-globular, slightly depressed Limnotrephini (sensu Polhemus 1990); body length 1.0–1.5 mm; yellowish with extended dark marks, which are irregular in some species of *Distotrephes* s. str.; lateral carina of cephalonotum continuous across eye, dividing it into a dorsal and a ventral part (in the hind-wing-brachypterous morph, Fig. 10), or widely extended onto eye surface, but not continuous (in the macropterous morph, Fig. 11); in dorsal view cephalonotum longer than the posterior part of the body; cephalonotum and mesoscutellum shining, with sparse and usually very fine punctation; hemelytron with coarser punctation and sparse, but quite long hairs; propleural plate at inner corner truncate; prosternal and metasternal carina simple; metasternal carina low, bifid, of the shape of a posteriorly open diamond; abdominal carina extended onto sternite 4; carina of sternite 2 anteriorly inserted in the structure of the metasternal carina; sternite 7 of female symmetrical (subgenus *Polhemotrephes*) or slightly to strongly asymmetrical (subgenus *Distotrephes*), at posterior margin emarginated (subgenus *Polhemotrephes*, Fig. 35), simple, or with a median process (subgenus *Distotrephes*, Figs 12–18); male genitalia: pygophore with sinistral process in most species of *Distotrephes* (except *D. jii* sp. n.), which is lacking in *Polhemotrephes*; aedeagus externally quite simple, with apex narrow (subgenus *Distotrephes*, e. g. Fig. 19) or broadly rounded (subgenus *Polhemotrephes*, Fig. 37); left paramere distally slender, apex either acuminate (subgenus *Distotrephes*, e. g. Figs 20, 29), or narrowly rounded (subgenus *Polhemotrephes*, Fig. 38); right paramere shorter than left paramere, apically acuminate, rounded, or truncate (subgenus *Distotrephes*, Figs 21, 24, 27, 30, 33, 34), or strongly reduced and acuminate (subgenus *Polhemotrephes*, Fig. 36); nymphs flattened.

DISCUSSION. Both subgenera are monophyletic groups with distinct characters in male genitalia and female subgenital plates. The lateral carina of the cephalonotum, which is (nearly) crossing the eye surface, the structure of the carinae on metasternum and sternite 2, the benthic habit, and probably also the long pilosity on the hemelytron are autapomorphies of the genus *Distotrephes* within the Limnotrephini.

MACROPTEROUS MORPHS. *Distotrephes* species have a wing dimorphism, with the hind-wing-micropterous morph much more frequent than the hind-wing-macropterous morph (mode a–c, after Papáček et al. 1989). The macropterous morph of *Distotrephes* is undescribed, although material was recorded by Zettel (1995, 1997). Macropterous specimens are externally recognizable by the presence of a claval suture and a separated embolium on the hemelytron, by a weak tubercle in the posterior corners of the cephalonotum, and in *Distotrephes* s. str. species also by an irregularly spotted hemelytron.

In the course of this study, surprisingly, an eye dimorphism was discovered (in five species belonging to both subgenera; see Tab. 1). In macropterous specimens, the eyes are larger and not completely divided by the lateral carina of the cephalonotum, which is related with the ability to fly. This eye dimorphism is so far undescribed in Helotrephidae, but was now proved also in *Trephotomas compactus* Papáček, Tonner et Štys, 1988, and is suspected for an undescribed *Fischertrephe* species, which is only known in the macropterous morph and differs by much larger eyes from other species (Zettel, in prep.). It is worth noting, that these are the three Oriental genera, which are – convergently, as belonging to three different subfamilies – most adapted to benthic habits, and subsequently have smaller eyes than genera living close to the water surface, where light conditions are better.

The eye index (minimum interocular distance / maximal eye width) was measured for species known in both morphs. Results are listed in Table 1.



Figs 1–9. Colour patterns of cephalonotum, frontal view, in (1–8) *Distotrephea* Polhemus s. str. and (9) *Polhemotrephe* Zettel; for explanations see text.

Table 1 Eye indices in *Trephotomas compactus* (from Hong Kong) and *Distotrephes* species, which are known in both, hind-wing-micropterous and macropterous morphs, numbers of specimens measured in brackets

Species	hind-wing-micropterous		macropterous	
	male	female	male	female
<i>T. compactus</i>	3.4–3.6 (3)	3.0–3.3 (3)	—	2.7 (1)
<i>D. styxi</i>	—	2.9–3.1 (3)	—	2.4 (1)
<i>D. asymmetricus</i>	—	2.9–3.0 (3)	—	2.4 (1)
<i>D. pavelistysi</i>	2.8–3.0 (3)	3.3–3.4 (3)	2.3 (1)	2.6–2.7 (3)
<i>D. shepardi</i>	2.8–2.9 (3)	3.1–3.3 (3)	—	2.5 (1)
<i>D. heveli</i>	3.4–3.5 (3)	3.5–3.6 (2)	—	3.1 (1)

SPECIES-DIAGNOSTIC CHARACTERS. *Distotrephes* species are very uniform in most characters, also in some features, which are often used for distinguishing species of other heliotrephid genera, e. g. size, body shape, ventral thoracic and abdominal carinae, and surface structures. The following characters are useful to distinguish *Distotrephes* species and subgenera.

Colour pattern: in the subgenus *Polhemotrephes* the cephalonotum is very uniformly coloured: nearly completely blackish brown on head and yellowish with dark hind corners on pronotum (Fig. 9). In *Distotrephes* s. str. the cephalonotum shows some variability in the distribution of the (dark) brown marks. The pattern on the head always consists of two median stripes, which may be confluent, especially anteriorly (in several species) (Figs 1–6), or interrupted, if the colour pattern is reduced (Figs 4–5); they are always medially separated in *D. styxi* and *D. ju* sp. n. (Figs 4–5, 7–8). Between these longitudinal stripes and the inner eye margin, there are additional marks: either a second pair of stripes (Figs 6–8) (in *D. styxi* and *D. asymmetricus*), or two pairs of spots, completely or partly separated by a transverse or triangular yellowish mark on inner eye margin (Figs 1–5) (in *D. laoticus* sp. n., *D. jii* sp. n., and *D. pavelistysi* sp. n.; indistinct in *D. shepardi* sp. n. and *D. schwendingeri* sp. n.). These two principal patterns are highly modified by the extension of the dark marks (sometimes intraspecific), but they are consistent. The pronotal colour pattern serves also for distinction of some species, i. e. it may be spattered and very irregular (e. g. in *D. styxi*) (Figs 7–8) or of clearer outlines (e. g. in *D. laoticus* sp. n.) (Fig. 2).

Colouration of mesoscutellum and hemelytra shows only small differences between species. The few macropterous *Distotrephes* s. str. specimens presently known are of quite dark head colouration within the limits of specific variability, and have spotted hemelytra.

Punctuation: the punctations of the cephalonotum and of the hemelytra are slightly different between species, and serve, beside colouration and size, as important characters to assign females to males.

Rostral length: the length of the labium is slightly varying between species and is useful to distinguish some species.

Sternal carinae: due to the depressed body, the sternal carinae are reduced. The shape of the metasternal "diamond" is broader in *Distotrephes* s. str. than in *Polhemotrephes*. The relative heights of prosternal and metasternal carinae may serve as a weak character for distinction of some species.

Sternite 7 (subgenital plate) of female: it is, beside male genitalia, the most important character for identification of subgenera and species. It is symmetrical and posteriorly emarginated in *Polhemotrephes* (Fig. 35), but more or less asymmetrical in *Distotrephes* s. str., where it possesses a median process in most species (except in *D. schwendingeri* sp. n.). The shape of the emargination or of the process, respectively, is most characteristic for the species (see Figs 12–18).

Male genitalia in most species of *Distotrepes* s. str. (except in *D. jii* sp. n.), the pygophore has a sclerotized, sinistral process which is useful for distinction of some species. It is lacking in *Polhemotrepes*.

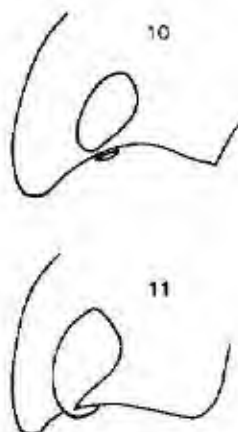
The aedeagus is less modified than in other helotrephid genera, although it serves for distinction of subgenera (comp. Figs 19 and 37); some species (e. g. *D. jii* sp. n.) may be recognized by the length of the vesica.

The left paramere is quite similar in most species of the same subgenus. In *Distotrepes* s. str. species the apical part is specifically bent or bowed (e. g. Figs 20, 26, 31, 32). In *D. (s. str.) jii* sp. n. the left paramere has an postero-medial "step" (Fig. 29), which is similarly developed in *Polhemotrepes* species (Fig. 38).

The right paramere of *Polhemotrepes* is strongly reduced and apically acuminate (Fig. 36). In *Distotrepes*, the distal part of the right paramere is diagnostic, its apex varying from acuminate or rounded to truncate (Figs 21, 24, 27, 30, 32, 34).

Key to subgenera and species of *Distotrepes* s. str.

- 1 Females 2
- Males (male of *D. laotus* sp. n. unknown). 9
- 2 Posterior margin of sternite 7 with median emargination (e. g. Fig. 35); three species from Borneo 9
- Posterior margin of sternite 7 without median emargination, either evenly rounded or with median lobe (Figs 12-18); species from the Southeast Asian mainland 3
- 3 Posterior margin of sternite 7 without lobe (Fig. 18); body length less than 1.2 mm (North Thailand) *D. schwendingeri* sp. n.
- Posterior margin of sternite 7 with distinct median lobe (Figs 12-17); body length more than 1.2 mm. 4
- 4 Sternite 7 strongly asymmetrical, with obliquely directed median lobe (Figs 12-13). 5
- Sternite 7 symmetrical or very slightly asymmetrical, with straight postward directed median lobe (Figs 14-17) 6



Figs 10-11. Eye and lateral carina of cephalonotum, antero-lateral view, in *Distotrepes pavelstysi* sp. n. from the same locality in Laos. (10) hind-wing-micropterous morph and (11) macropterous morph. In the large eyed macropterous specimen the lateral carina is not continuous across eye.

- 5 Median lobe of sternite 7 with broad base, less oblique (Fig. 12); colour pattern of head as in Figure 6 (Southeast China). *D. asymmetricus*
- Median lobe of sternite 7 with slender base, strongly oblique (Fig. 13); colour pattern of head as in Figure 2 (North Laos). *D. laoticus* sp. n.
- 6 Median lobe of sternite 7 broad, shorter than wide, and distally rounded (Figs 14, 15). 7
- Median lobe of sternite 7 slender, at least as long as wide, and distally truncate (Figs 16, 17). 8
- 7 Punctures laterally on pronotum and on hemelytra coarser and denser, dark pattern on head reduced, consisting of spots (Figs 4, 5) (China, Hainan). *D. ju* sp. n.
- Punctures laterally on pronotum and on hemelytra finer and sparse; dark pattern on head more developed, consisting of four (sometimes broken) longitudinal lines (Figs 7, 8) (Southeast China, including Hainan). *D. styxi*
- 8 Median lobe of sternite 7 slightly longer (Fig. 17); head colouration usually without triangular yellow marks at inner eye margin (North Thailand). *D. shepardi* sp. n.
- Median lobe of sternite 7 slightly shorter, less pronounced (Fig. 16); head colouration usually with distinct triangular yellow marks at inner eye margin (North Thailand, North Laos). *D. pavelstysi* sp. n.
- 9 Right paramere strongly reduced, half as long as left paramere or shorter, always with acute apex (e. g. Fig. 36), left paramere of typical structure as in Fig. 38, three species from Borneo. subgenus *Polhemotrephes*
- Species are distinguishable only by male genitalia, which were figured by Zettel (1995, 1997)
- Right paramere only slightly shorter than left paramere; left paramere of different shape (e. g. Figs 20, 23), only in one species with postero-medial step (Fig. 29); species from the Southeast Asian mainland. subgenus *Distotrephes* s. str. ... 10
- 10 Right paramere distally more or less widened, apically broad and truncate (Figs 33, 34). 11
- Right paramere distally parallel-sided or tapered, apically slender, acute or rounded (Figs 21, 24, 27, 30). ... 12
- 11 Left paramere with slender base, apically distinctly bent (Fig. 32); right paramere apically broader (Fig. 33); prosternal keel distinctly higher than mesosternal keel, rostrum not reaching the posterior end of prosternal keel (Southeast China). *D. asymmetricus*
- Left paramere with broad base, apically nearly evenly bowed (Fig. 31); right paramere apically more slender (Fig. 34), prosternal keel about as high as mesosternal keel, rostrum slightly surpassing posterior end of prosternal keel (Southeast China, North Viet Nam). *D. styxi*
- 12 Apex of right paramere acute (Fig. 30); left paramere with step in middle of length, and with bent apex (Fig. 29), aedeagus with long vesica, which partly exposed from the phallus (Fig. 28) (China: Hainan). ... *D. ju* sp. n.
- Apex of right paramere rounded; left paramere without step in middle of length, and with less distinctly bent or evenly bowed apex; aedeagus with short vesica, which not exposed from the phallus (species from North Thailand and North Laos). 13
- 13 Process of pygophore short and rounded, right paramere less elongate and bowed in distal half (Fig. 27); left paramere slightly bent apically (Fig. 26), body length less than 1.2 mm. *D. schwendingeri* sp. n.
- Process of pygophore longer and truncate; right paramere elongate and nearly straight in distal half (Figs 21, 24); left paramere nearly evenly bowed apically (Figs 20, 23); body length more than 1.2 mm. 14
- 14 Right paramere very slender, apically evenly rounded (Fig. 24); head colouration (usually) without triangular yellow marks at inner eye margin. *D. shepardi* sp. n.
- Right paramere slightly broader, apically not evenly rounded, but slightly obliquely-truncate (Fig. 21); head colouration usually with distinct triangular yellow marks at inner eye margin. *D. pavelstysi* sp. n.

DESCRIPTIONS OF NEW SPECIES

Distotrephes (s. str.) *pavelstysi* sp. n.

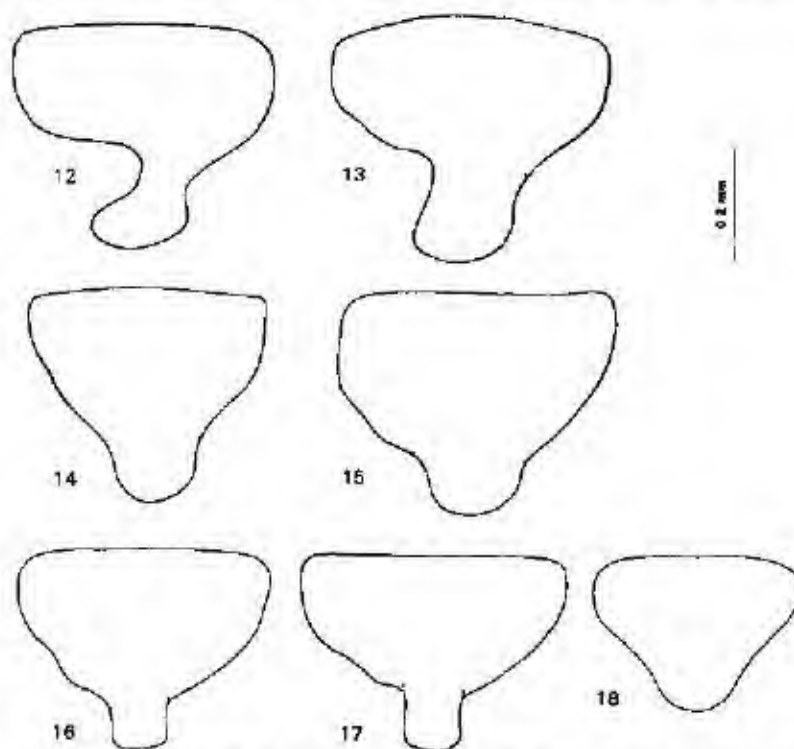
(Figs 10, 11, 16, 19–21)

TYPE MATERIAL. Holotype (male): "Thailand, Chiang Mai\ Doi Sut[h]ep NP, Wang Bua\ Boo, 24.III.1994\ leg. W.D. Shepard (1042)" (NMW). Paratypes: 1 male, 5 females, 1 female (macropterous), same locality data (CSS, CHMU, JTPC, NMW), 2 females "Thailand: Chiang Mai\ Doi Sut[h]ep NP, Montatharn\ Falls, 24.III.1994\ leg. W.D. Shepard (1044)" (NMW); 1 male "Thailand, Chiang Mai\ Doi Sut[h]ep Nat. Park\ 24.III.1994\ Huai Sa Lad\ WDS-A-1043", "William D\ Shepard, leg." (CSS); 1 female "Thailand, Chiang Mai Prov\ Doi Suthep NP, Montatharn\ Falls, 700–750m, 6.II.1995\ leg. H. Zettel (8)" (NMW); 1 male, 1 female "Thailand: Mae Hong Son Prov\ 3 km SE Mae Hong Son, 13.II.1995\ leg. H. Zettel (14b)" (NMW), 1 male "Fang, Thailand\ Nov. 21, 1968\ M. Satō leg." (JTPC); 1 male, 1 female (both macropterous) "LAOS Luang Nam Tha Pr\ 20km SE Muang Sing\ 950m, 12.6.1996\ leg. Schilhammer (25); 1 male, 1 female (macropterous) "N LAOS\ Luang Namtha env.\ 800–1200 m\ May 1997" (NMW).

DESCRIPTION. Size: body length 1.25–1.37 mm in micropterous specimens, 1.42–1.48 mm in macropterous specimens; body width 0.91–1.11 mm in micropterous specimens, 1.09–1.12 mm in macropterous specimens, micropterous females (length 1.29–1.37 mm) in average larger than micropterous males (length 1.25–1.34 mm).

Colour: cephalonotum yellow with large light to dark brownish marks on head, consisting of five large, confluent spots similar to Fig. 2, but yellow mark on inner eye margin triangular and anterior dark mark never reaching apex of head or even absent, spots rarely larger (similar as in Fig. 3); pronotal part usually with four (two medial, two in hind corners) more or less extended, irregular brownish marks; mesoscutellum yellowish with irregular brownish marks of varying extension; hemelytron dark brownish, with yellow postero-lateral margin and a yellowish spot at lateral margin of mesoscutellum; ventrally on head and prothorax yellow, on meso- and metathorax and on abdomen brown; legs yellow; macropterous specimens more colourful, with contrastingly marked, irregular dark brown and yellow patterns on pronotum, mesoscutellum, and corium of hemelytron.

Eye indices see Table 1; eye of macropterous specimen not completely divided by the lateral margin of the cephalonotum; cephalonotum and mesoscutellum shining; punctation of head and medial part of pronotum very fine and sparse; punctures of pronotum laterally and mesoscutellum rather fine, irregularly spaced on pronotum, widely spaced on mesoscutellum; hemelytron with rather large punctation, distance between punctures usually more than 2.0 times (often up to 4



Figs 12–18. Sternites 7 of females of *Distotrephes* Polhemus s. str. species: (12) *D. laoticus* sp. n., (13) *D. asymmetricus* Zettel, (14) *D. ju* sp. n., (15) *D. styxi* Polhemus, (16) *D. pavelistyi* sp. n., (17) *D. shepardi* sp. n., (18) *D. schwendingeri* sp. n.

times) their diameter, between punctures soap-shiny, with reduced or sometimes faintly visible micro-reticulation at magnification of 120 \times , hemelytron of macropterous specimen with separated clavus and embolium, more shining and punctures more widely spaced

Rostrum reaching the posterior corner of the prosternal carina, which is slightly higher (rarely distinctly higher) than the mesosternal carina

Male genitalia pygophore with a relatively long, apically obliquely truncate process on its left side, aedeagus (Fig. 19) with slender, nearly straight apex and vesica not exposed from the phallus, left paramere (Fig. 20) rather evenly curved, relatively slender in middle of its length, evenly tapered toward the acuminate apex, subapically often with a row of fine hairs, right paramere (Fig. 21) slender, parallel-sided, and nearly straight in middle part, with a narrowly and obliquely truncate apex

Female sternite 7 (Fig. 16) nearly symmetrical, with very pronounced, slender, apically truncate postero-median lobe

VARIABILITY There are only small differences between the populations studied, which may be individual deviations as only a few specimens were collected in Mae Hong Son and Luang Nam Tha: left paramere in males from Laos without row of hairs posteriorly, tip of right paramere in male from Mae Hong Son less obviously obliquely-truncate, female from Mae Hong Son with a shorter, apically less truncate postero-median process on sternite 7. More material will have to be studied before splitting *D. pavelstysi* sp. n. into possible, regional, infraspecific units

COMPARATIVE NOTES *Distotrephes pavelstysi* sp. n. is very closely related with *D. shepardi* sp. n. (differences see there), based on male genitalia and female sternite 7. Shape of both male parameres are diagnostic

DISTRIBUTION Thailand: Chiang Mai, Mae Hong Son, Laos: Luang Nam Tha

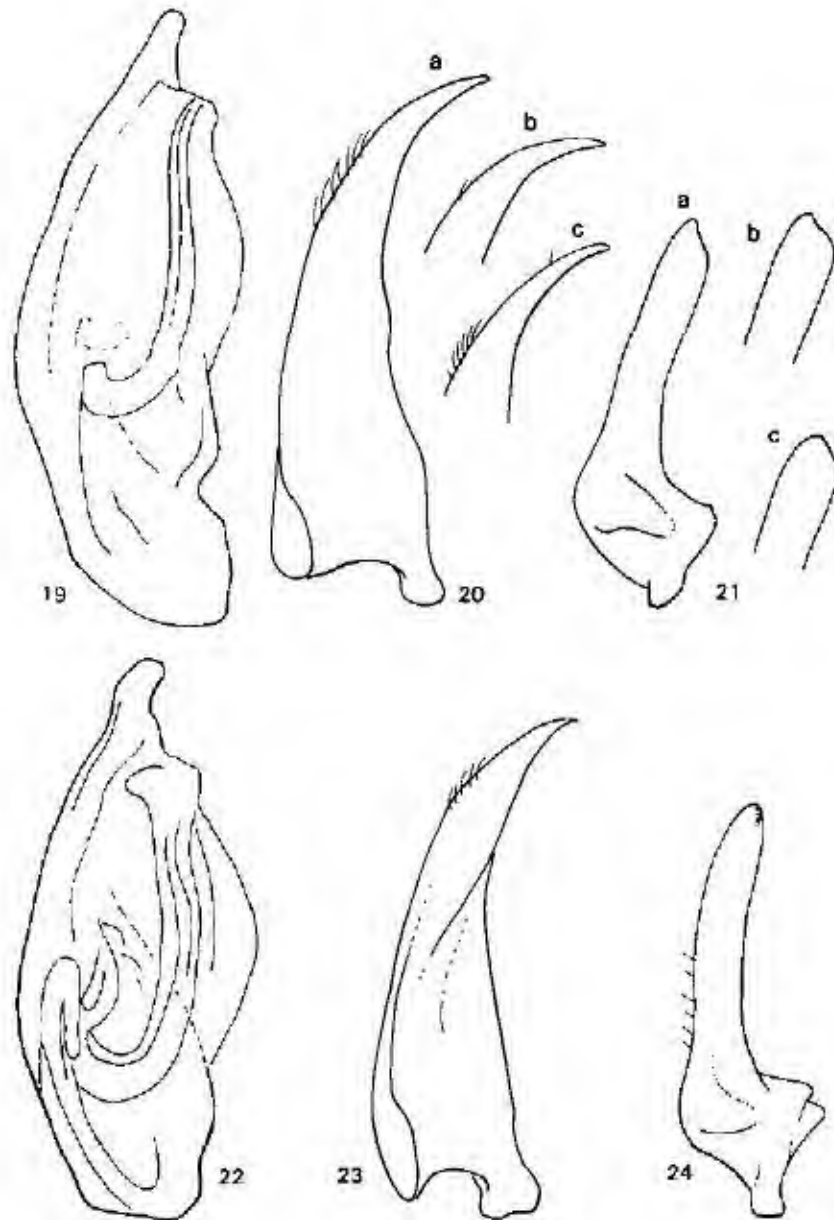
ETYMOLOGY Named in honour of Prof. Dr. Pavel Štys (Charles University, Praha, Czech Republic) on the occasion of his 65th birthday

***Distotrephes* (s. str.) *shepardi* sp. n.**
(Figs 17, 22–24)

TYPE MATERIAL: Holotype (male): "Thailand: P[h]etchabun\ 36km SE Sila, Huai Nam\ Phang, 2 III 1994\ leg. W.D. Shepard (1024)" (NMW); paratypes: 1 male, 4 females, 1 female (macropterous) same locality data (NMW, CSS); 1 male, 1 female "Thailand: P[h]etchabun\ Nam Nao NP, Prom Laeng\ 27 III 1994\ leg. W.D. Shepard (1040)" (NMW); 2 females "Thailand: P[h]etchabun\ Nam Nao NP, Huai Ya\ Krua, 14 III 1994\ leg. W.D. Shepard (1039)" (NMW, CSS); 1 male, 7 females "Thailand: Phetchabun Prov\ Nam Nao NP, Huai Phrom\ Laeng, 24 II 1995\ leg. H. Zettel (22)" (NMW, CNT, JTPC, KKUA); further material: 2 ex. (abdomen and legs partly missing), 1 larva, same locality data as holotype (CSS)

DESCRIPTION: Size: body length 1.21–1.35 mm in micropterous specimens, 1.44 mm in macropterous female, body width 0.88–1.02 mm in micropterous specimens, 1.09 mm in macropterous female, micropterous females (length 1.24–1.35 mm) on average larger than males (length 1.21–1.26 mm)

Colour: cephalonotum yellow with large brownish to blackish marks on head, consisting of five large, confluent spots similar to Fig. 1, but anterior mark rarely reaching apex of abdomen, very rarely more separated (but not as much as in Fig. 2), pronotal part with usually four (two medial, two in posterior corners) more or less extended, irregular brownish marks, mesoscutellum yellowish with irregular brownish marks, hemelytron dark brownish, with yellow postero-lateral margin and a yellowish spot at lateral margin of mesoscutellum, ventrally on head and prothorax yellow, on meso- and metathorax and on abdomen brown, legs yellow, macropterous specimen more colourful, with contrastingly marked, irregular dark brown and yellow pattern on pronotum, mesoscutellum, and corium of hemelytra



Figs 19-24: Male genitalia of *Dustorephes pavelstysi* sp. n. (19-21): (19) aedeagus, (20) left parameres (a: from Laos, b: from Mae Hong Son, c: from Doi Suthep), (21) right parameres (a: from Chiang Mai, b: from Laos, c: from Mae Hong Son); and of *D. shepardi* sp. n. (22-24): (22) aedeagus, (23) left paramere, (24) right paramere; all in right view.

Eye indices see Table 1; eye of macropterous specimen not completely divided by the lateral margin of the cephalonotum; cephalonotum and mesoscutellum shining; punctation of head and medial part of pronotum very fine and sparse; punctures of pronotum laterally and mesoscutellum medium-sized, irregularly spaced on pronotum, widely spaced on mesoscutellum; hemelytron with rather large punctation, distance between punctures usually more than 2.0 times (often up to 4 times) their diameter, between punctures soap-shiny, with reduced micro-reticulation at magnification of 120 \times ; hemelytra of macropterous specimen with separated clavus and embolium, more shining and punctures more widely spaced.

Rostrum slightly surpassing the posterior corner of the prosternal carina, which is not distinctly higher than the mesosternal carina.

Male genitalia: pygophore with a relatively long, apically obliquely truncate process on its left side; aedeagus (Fig. 22) with relatively stout, slightly bent apex and vesica not exposed from the phallus; left paramere (Fig. 23) rather evenly curved, relatively stout in middle of its length, apically strongly tapered, subapically with a row of fine hairs, and with acuminate apex; right paramere (Fig. 24) very slender, parallel-sided, and nearly straight in middle part, with a narrowly rounded apex.

Female sternite 7 (Fig. 17) nearly symmetrical, with very pronounced, slender, apically truncate postero-median lobe.

COMPARATIVE NOTES. *Distotrephes shepardi* sp. n. is most closely related with *D. pavelstysi* sp. n., with which it shares similar structures of male genitalia and female sternite 7. Small differences between species are constant: in *D. shepardi* sp. n. the aedeagus with relatively broad apex (comp. Figs 19 and 22), the left paramere subapically broad, then strongly and not so evenly tapered (comp. Figs 20 and 23), the right paramere apically relatively slender, with narrowly rounded apex (comp. Figs 21 and 24), and the colour pattern of head darker (although there is a small overlapping in the extension of the patterns of both species). Whether these differences are specific or subspecific cannot be decided from the present knowledge. It seems that both species are allopatric. *Distotrephes shepardi* sp. n. is only known from the Nam Nao NP, an area which has a fauna distinctly different from that of the Chiang Mai region. From *D. schwendingeri* sp. n., which is distributed in the same area, *D. shepardi* sp. n. can be distinguished – beside the striking sexual characters – by larger size and finer punctation of the lateral parts of the cephalonotum.

DISTRIBUTION. Thailand: Phetchabun.

ETYMOLOGY. Named in honour of Prof. Dr William D. Shepard (Sacramento, U. S. A.) for providing me with this and numerous other interesting helotrephid species from Thailand and Malaysia.

Distotrephes (s. str.) *jii* sp. n. (Figs 14, 28–30)

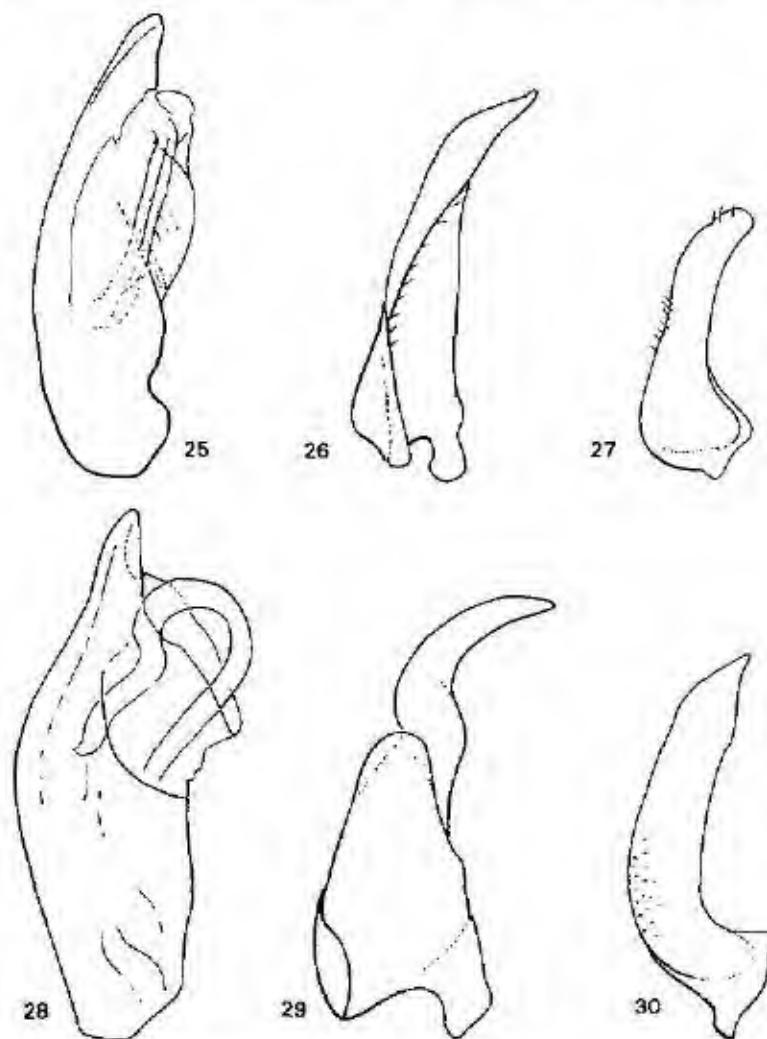
TYPE MATERIAL. Holotype (male): "CHINA: Hainan (194) 30km E Maoyang, 18.1. Wuzhi Shan Resort, 1996\ 700–800m, Ji & Wang" (NMW); paratypes: 1 male, same locality data (CASS); 1 female "CHINA: Hainan (193) 30km E Maoyang, 600m\ Wuzhi Shan Resort, 1996\ 17.18.1., Ji & Wang" (NMW); 1 female "CHINA: Hainan (188) 7km W Gongzhong\ Baihua Ling, 300m\ 16.1.1996, leg. Jäch" (NMW); 1 male "Lanyang\ Hainan, China\ 25 – IV – 1994\ M. Satô leg." (JTPC); further material: 1 female (all legs missing, sternite 7 broken) "CHINA: Hainan (197) 3km E Maoyang, 200m\ Wuzhi Shan Riv.\ 19.1.1996, Ji & Wang" (NMW).

DESCRIPTION. Size: body length 1.32–1.40 mm; body width 0.97–1.06 mm.

Colour: cephalonotum yellow with reduced light brownish marks on head, two interrupted medial longitudinal stripes and two pairs of spots at inner eye margin (comp. Figs 4–5), which are rarely more extended, and with very small, faint marks on pronotal part; mesoscutellum yellowish with irregular brownish marks; hemelytron dark brownish, with yellow postero-lateral margin and a yellowish spot at lateral margin of mesoscutellum; ventrally light brown to yellowish; legs yellow.

Cephalonotum and mesoscutellum shining; punctation of head and medial part of pronotum very fine and sparse; punctation of pronotum laterally coarse, irregularly spaced, punctures as large as on hemelytron; punctures on mesoscutellum of same size, but very widely spaced; hemelytron with large punctation, distance between punctures in an average about 1.5 times their diameter, between punctures soap-shiny, without distinct micro-reticulation at magnification of 120 \times ; all specimens hind-wing-micropterous.

Rostrum hardly reaching the posterior corner of the prosternal carina, which is angulate and distinctly higher than the mesosternal carina; carina of sternite 2 relatively high.



Figs 25-30: Male genitalia of (25-27) *Diatotrephes schwendingeri* sp. n. and of (28-30) *D. jii* sp. n.: (25, 28) acedeagus, (26, 29) left paramere, (27, 30) right paramere; all in right view.

Male genitalia: pygophore without process on its left side; aedeagus (Fig. 28) with narrow tip and vesica exposed from the phallus; left paramere (Fig. 29) with posterior step in middle of its length, with strongly curved distal part, and with acuminate apex; right paramere (Fig. 30) parallel-sided in middle part, with acute apex.

Female sternite 7 (Fig. 14) with short, rounded median lobe, nearly symmetrical.

COMPARATIVE NOTES. *Distotrephes jii* sp. n. differs from all other species of the subgenus in the lack of a pygophore process and a characteristic step posteriorly on left paramere. Otherwise *D. jii* sp. n. is similar to *D. pavelstysi* sp. n. and *D. shepardi* sp. n., e. g. in the apically tapered right paramere and differs from these species by the following characters: left paramere distally strongly curved, right paramere with acute apex, aedeagus with exposed vesica, and female subgenital plate distally broader. Hainan Island is also inhabited by *D. styxi* (see below), which differs strongly in male genitalia. However, females have very similar subgenital plates; they can be distinguished by a coarser punctation on the lateral parts of the pronotum of *D. jii* sp. n. Further, the dark head colouration of *D. styxi* is not as much reduced as in *D. jii* sp. n.

DISTRIBUTION. China: Hainan.

ETYMOLOGY. Named in honour of Prof. Lanzhu Ji (Shenyang, China), who collected a part of the type series.

***Distotrephes* (s. str.) *schwendingeri* sp. n.**
(Figs 18, 25–27)

TYPE MATERIAL. Holotype (male): "Thailand: Phetchabun\ 36km SE Sila, Huai Nam\ Phang, 2.III.1994\ leg. W.D. Shepard (1024)" (NMW); paratypes: 1 male, same locality data (NMW); 2 females "Thailand: Phrac Prov.\ 50km NE Phrac, Huai Kaet\ Kaet river, 17.–18.II. 1995, leg. H. Zettel (17b)" (NMW); further material: 1 larva, same locality data as female paratypes (NMW).

DESCRIPTION. Size: body length 1.08–1.13 mm; body width 0.75–0.78 mm.

Colour: cephalonotum yellow with extended brown marks on head consisting of five confluent spots similar as in Fig. 3 or slightly more reduced (similar to Fig. 2), and with brownish marks on posterior corners of pronotal part; mesoscutellum yellowish without or with faint brownish marks; hemelytron dark brownish, with yellow postero-lateral margin, in one female with an indistinct yellowish spot at the lateral margin of the mesoscutellum; ventrally on head and prothorax yellow, on meso- and metathorax and on abdomen brown; legs yellow.

Cephalonotum and mesoscutellum shining; punctation of head very fine and sparse, of medial part of pronotum and mesoscutellum medium sized and widely spaced; punctation of pronotum laterally coarse, irregularly spaced, punctures as large as on hemelytron; hemelytron with large punctation, distance between punctures nearly everywhere more than 2.0 times their diameter, in some areas up to 4.0 times, between punctures soap-shiny, without distinct micro-reticulation at magnification of 120 \times ; all specimens hind-wing-micropterous.

Rostrum not reaching the posterior corner of the prosternal carina, which is slightly higher than the mesosternal carina.

Male genitalia: pygophore with short, rounded process on its left side; aedeagus (Fig. 25) with rather broad apex and vesica not exposed from the phallus; left paramere (Fig. 26) slightly bent, with acuminate apex; right paramere (Fig. 27) finger-shaped, slightly bowed in medial part, with rounded apex.

Female sternite 7 (Fig. 18) without distinct medial lobe, more evenly rounded on posterior margin, nearly symmetrical.

COMPARATIVE NOTES. Males and females, although from different localities, are regarded as conspecific, because of the very small size (1.08–1.13 mm, males slightly smaller than females), coarse punctuation on the lateral parts of the pronotum, and an identical colour pattern. The female of *D. schwendingeri* sp. n. is very easy to identify by the striking different subgenital plate: In all other species of the subgenus it bears a postero-medial process, whereas the subgenital plate of *D. schwendingeri* sp. n. has a nearly evenly rounded hind margin (Fig. 18). The male has diagnostic genitalia, especially the right paramere, which is relatively short, slightly bowed, and apically rounded (Fig. 27). The aedeagus (Fig. 25) has the broadest apex of all species of the subgenus.

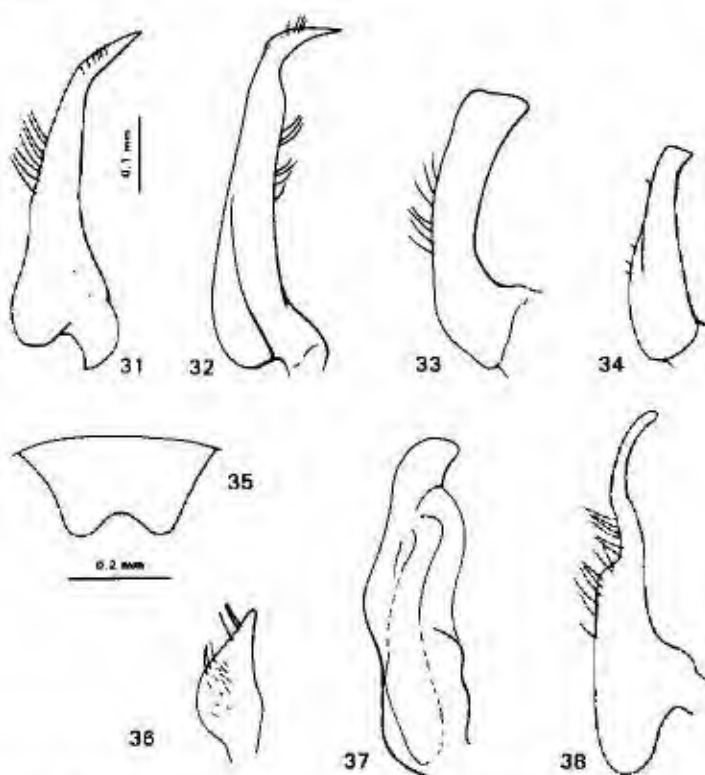
DISTRIBUTION. Thailand: Phetchabun, Phrae.

ETYMOLOGY. Named in honour of Dr Peter Schwendinger, arachnidologist at the University of Innsbruck (Austria), for "guiding" me to the locality in Phrae province.

***Distotrephes* (s. str.) *laoticus* sp. n.**

(Fig. 12)

TYPE MATERIAL. Holotype (female): "N LAOS, Luang Namtha env., 800–1200 m, May 1997" (NMW); paratype: 1 female same locality data (NMW).



Figs 31–38: Left (31, 32) and right (33, 34) parameres of (31, 34) *Distotrephes styxi* sp. n. and (32, 33) *D. asymmetricus* Zettel; *D. (Polhemotrephes) sarawakensis* Zettel (35–38): (35) sternalite 7 of female, ventral view (in situ), (36) right paramere, (37) aedeagus, (38) left paramere; all genitalia in right view (all from Zettel 1995).

DESCRIPTION. Size: body length 1.38–1.41 mm, body width 1.05–1.06 mm.

Colour: cephalonotum yellow with distinct blackish colour pattern, with marks on head as in Figure 2 or similar, with large yellowish spots at the middle of inner eye margin, and on the pronotal part with a transverse blackish band, which is laterally connected with a second, narrower band along the hind margin, mesoscutellum yellow with brown marks, hemelytron blackish brown with yellow postero-lateral margin and with a yellowish spot at the lateral margin of the mesoscutellum, ventrally on head and prothorax yellow, on meso- and metathorax and on abdomen brown, legs yellow.

Cephalonotum and mesoscutellum shining, punctation of head, medial part of pronotum, and mesoscutellum very fine and sparse; punctation of pronotum laterally slightly coarser, widely spaced, punctures slightly finer than those on the hemelytron, hemelytron with rather large punctation, distance between punctures in an average more than 2.0 times their diameter, between punctures soap-shiny, without distinct micro-reticulation at magnification of 120 \times , both specimens hind-wing-micropterous.

Rostrum reaching the posterior corner of the prosternal carina, which is not higher than the mesosternal carina, metasternal carinae posteriorly less convergent, forming more a pentagonal than a diamond-shaped structure.

Female sternite 7 (Fig. 12) very asymmetrical, with a long median lobe, which is obliquely directed to the right side, narrow at base and then widened.

COMPARATIVE NOTES. The female of *D. laoticus* sp. n. has a very characteristic, extremely asymmetrical sternite 7 with a very oblique median lobe (Fig. 12). It differs from *D. asymmetricus* in the shape of this lobe, which is distinctly broader in *D. asymmetricus* (Fig. 13) than in *D. laoticus* sp. n., and by a different colour pattern of the cephalonotum (see key).

DISTRIBUTION. Laos: Luang Nam Tha.

ETYMOLOGY. Named after its country of origin, Laos.

NOTES ON OTHER SPECIES

Distotrephes (s. str.) *stysi* Polhemus, 1990

(Fig. 15, 31, 34)

FURTHER MATERIAL EXAMINED (see also Zettel 1995): 4 males, 4 females "CHINA: FUJIAN, Chong'an: Wuyi Shan, 3 km NW Wuyi Gong, 300m, 17 I 1997, leg. Ji & Wang (CWBS 246)" (NMW, CASS, CPC, JTPC), 1 male "CHINA: FUJIAN, Guangze: Wuyi Shan, 12 km S Zhuma: Li Fang, 400 m, 22 I 1997, leg. Ji & Wang (CWBS 252)" (NMW), 1 male "CHINA: FUJIAN, Longyan: Jiagushan (20 km N Longyan): Keshan monastery, 900m, Mohe Shan, 28 I 1997, leg. Ji & Wang (CWBS 260)" (NMW), 1 male "CHINA: FUJIAN, Chong'an: Wuyi Shan, 1 km W Wuyi Gong, 250m, 15/18 I 1997, leg. Ji & Wang (CWBS 240)" (NMW), 1 male "CHINA: Hainan (189): 7km W Qiongzong: Baohua Ling, 300m, 16 I 1996, leg. Ji" (NMW), 3 males, 1 female "Tongzai: Hainan, China: 29-IV-1994: M. Sato leg." (JTPC).

NOTES. This species was so far recorded from North Viet Nam (Vinh Phu) and from South China (Hunan and Hong Kong). New records for Fujian and Hainan.

Eye indices for both morphs see Table 1. All specimen measured are from Hong Kong (locality cited in Zettel 1995).

Distotrephes (s. str.) *asymmetricus* Zettel, 1995

(Figs 13, 32, 33)

FURTHER MATERIAL EXAMINED (see also Zettel 1995): 2 males, 2 females "CHINA: FUJIAN, Yong'an: 5 km SW Xiyang, 550m, Ziyungdong Shan, 25 I 1997, leg. Ji & Wang (CWBS 256)" (NMW), 2 males, 1 female "CHINA: Anhui,

Huang Shan\ 30km NW Tunxi, 24.10.1997\ Qi Yun Shan, 250m\ leg. Schönmann (CWBS 285)" (NMW); 5 females "CHINA: Anhui, Huang Shan\ 40km NW Tunxi, 26.10.1997\ rd. to Tang Kou, 350–400m\ leg. Schönmann (CWBS 287)" (NMW, CPC, JTPC); 1 female (macropterous) "CHINA: Anhui, Huang Shan\ 30km NW Tunxi, 28.10.1997\ 5km E Nantang, 350–400m\ leg. Schönmann (CWBS 288)" (NMW); 4 males, 4 females "CHINA: Anhui, Huang Shan\ 50km NW Tunxi, 29.10.1997\ Yi Xian Shan, 350–400m\ leg. Schönmann (CWBS 290)" (NMW, CASS, CPC); 1 male "CHINA: Anhui, Huang Shan\ 30km NW Tunxi, 30.10.1997\ 3km W Nantang, 350–550m\ leg. Schönmann (CWBS 291)" (NMW); 2 females "CHINA: Anhui, Dabie Shan\ 40km N Yuexi, 5.11.1997\ env. Gui Xing Di, 800m\ leg. Schönmann (CWBS 295)" (NMW).

NOTES. This species has been described from the South Chinese provinces Hunan and Guangxi. New records for Fujian and Anhui.

The macropterous morph was so far unknown. Eye indices for both morphs see Table 1. All specimen measured are from Anhui.

Distotrepes asymmetricus and *D. stysi* live sympatrically in Southeast China, but so far the species have never been found to be syntopic. No differences in habitat preferences could be worked out from the field notes by H. Schönmann (NMW), who studied the collecting sites in Hunan, Guangxi, Fujian, and Anhui. There is also no significant difference in altitude distribution; collecting data are ranging from 250 to 900 m a. s. l. in *D. stysi*, and from 150 to 800 m a. s. l. in *D. asymmetricus*.

CORRECTION. Due to a typing error in the original description (Zettel 1995), the holotype was wrongly designated as a female, but it is a male.

Distotrepes (Polhemotrepes) heveli Polhemus, 1990

MATERIAL EXAMINED. See Zettel (1995, 1997).

NOTES. Eye indices for both morphs see Table 1. All specimen measured are from the Crocker Range, Sabah (locality cited in Zettel 1997).

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Genus *Malcus* in China, with description of phallic structures (Hemiptera – Heteroptera: Malcidae)

Le-yi ZHENG

Department of Biology, Nankai University, Tianjin 300071, Peoples' Republic of China

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Abstract. So far known distributional data of 21 species of the genus *Malcus* Stål, 1859, recorded from China, are summarized and mapped. Phallic structures of *M. dentatus* Štys, 1967, *M. elongatus* Štys, 1967, *M. flavidipes* Stål, 1859, *M. setosus* Štys, 1967, and *M. sinicus* Štys, 1967 are described and illustrated. Biological notes on the genus and data on foodplants of some species are provided.

Distribution, morphology, phallus, foodplants, Heteroptera, Malcidae, *Malcus*, Palaearctic region, Oriental region

INTRODUCTION

The present paper is dedicated to Prof. Pavel Štys, for his outstanding contributions to the studies of Heteroptera, including Malcidae.

A list of *Malcus* Stål, 1859 species, hitherto known from China, with distribution data and maps, descriptions and illustrations of phallic structures of five species, data on foodplants and other notes on biology are provided in the present paper.

Species *Malcus idoneus* from Taiwan was as first Chinese record of *Malcus* published by Horváth (1914). Štys (1967) described new species, *M. inconspicuus*, *M. insularis*, and *M. sinicus*, and recorded *M. flavidipes* from China in his monumental monograph of Malcinae (Malcidae). Zheng, Zou & Hsiao (1979) described seven new *Malcus* species from China. Later on Zheng & Zou (1981a) included data on 18 species, and at least some records were published by Zheng & Zou (1981b) and Zheng (1988).

Concerning the structure of phallus, Štys (1967) described the general phallus features of the genus *Malcus* in detail, and provided excellent figures of the phallus of *M. furcatus*. He compared the *Malcus* phallus with phalli of related groups and extensively discussed its phylogenetic significance.

The phalli of five *Malcus* species, *M. dentatus*, *M. elongatus*, *M. flavidipes*, *M. setosus*, and *M. sinicus*, are described and illustrated. The results are compared with description of *M. furcatus* by Štys (1967).

MATERIAL AND METHODS

The greater part of the distributional data are based on material from a collection of the Nankai University, Tianjin, if not mention otherwise. All Taiwan records refer to Štys (1967).

The most of the dissected phalli are only partly inflated, was necessary to help them by pincette to stretch. However, the main features are all clearly visible, also in this state of phallus, is possible to compare particular phalli. The orientations, and views, used in the descriptions, and the figures, follow Štys's (1967) description and illustrations.

LIST OF SPECIES AND DISTRIBUTION

Malcus arcuatus Zheng, Zou et Hsiao, 1979

(Fig. 5)

MATERIAL. Fujian Prov.: Jian-yong Co. (Huang-keng [27°50'N, 117°60'E]).

Malcus auriculatus Štys, 1967

(Fig. 3)

MATERIAL. Hunan Prov.: Sang-zhi Co. (Mt. Tian-ping [29°30'N, 110°10'E]). Guangxi Prov.: Long-sheng Co. [25°70'N, 110°00'E]. Sichuan Prov.: Mt. Omei [29°50'N, 103°30'E]; Guan-xian Co. (Mt. Qing-cheng [30°90'N, 103°50'E]). Guizhou Prov.: Li-bo Co. [25°40'N, 107°80'E]. Yunnan Prov.: Teng-chong Co. [25°00'N, 98°50'E]; Ping-bian Co. (Mt. Da-wei [22°90'N, 103°70'E]).

Malcus dentatus Štys, 1967

(Fig. 3)

MATERIAL. Yunnan Prov.: Jing-hong Co. (Da-Meng-Long [21°50'N, 100°60'E]); Meng-la Co. (Meng-la [21°40'N, 101°50'E]); Shang-yong [21°20'N, 101°70'E]).

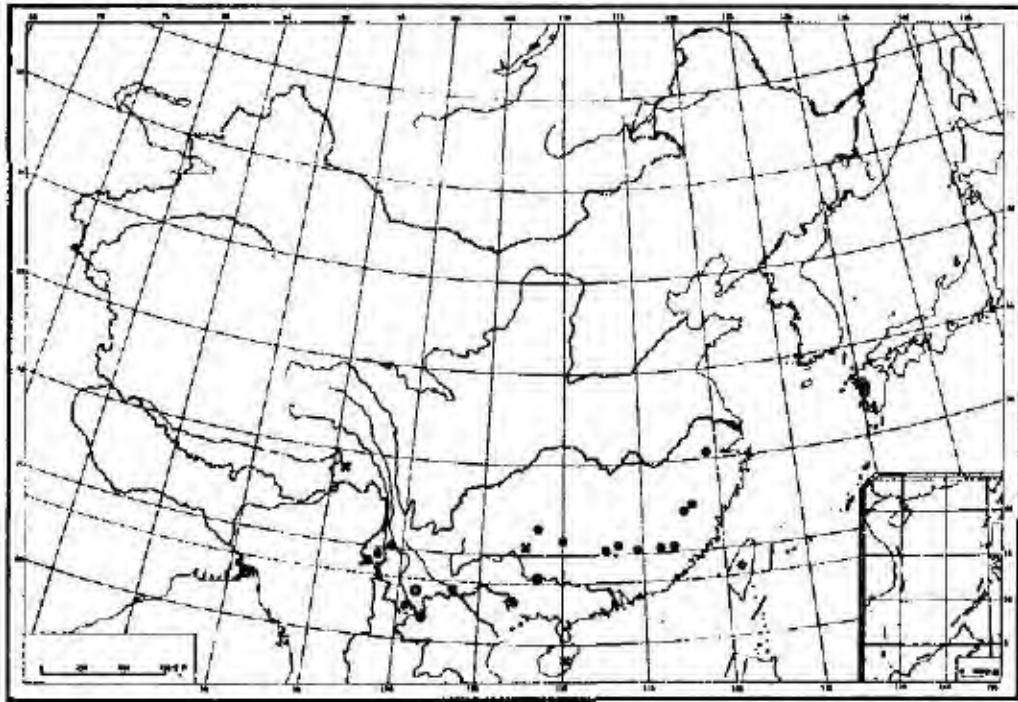


Fig. 1. Distribution of *Malcus* spp. in China. ● — *M. elongatus* Štys, ◐ — *M. gibbus* Zheng, Zou et Hsiao, ◆ — *M. insularis* Štys, * — *M. nigrescens* Štys.

***Maltus denticulatus* Štys, 1967**

(Fig. 3)

MATERIAL. **Hubei Prov.:** Yi-du Co. (Hong-Hua [30°40'N, 111°30'E]); Fang-xian Co. (Qiao-shang [31°90'N, 110°70']). **Jiangxi Prov.:** Mt. Lu-shan [29°40'N, 115°90'E]. **Fujian Prov.:** Chong-an Co. (San-gang [27°70'N, 117°70'E]); Long-yan Co. (Yong-he [24°80'N, 117°00'E]). **Sichuan Prov.:** Mt. Qing-cheng [30°90'N, 103°50'E]; Ya-an Co. (Mt. Zhou-gong [29°90'N, 102°90'E]); Bao-xin Co. (Baixin [30°30'N, 102°80'E], alt. 940–1340 m).

***Maltus elevatus* Zheng, Zou et Hsiao, 1979**

(Fig. 2)

MATERIAL. **Guangxi Prov.:** Ping-xiang Co. [22°10'N, 105°70'E]. **Guizhou Prov.:** Li-bo Co. (Mao-lan [25°30'N, 108°00']).

***Maltus elongatus* Štys, 1967**

(Fig. 1)

MATERIAL. **Zhejiang Prov.:** Mt. Tian-mu [30°40'N, 119°50'E]. **Fujian Prov.:** Jian-yang Co. (Huang-keng [27°50'N, 117°60'E]); Long-yan Co. (Yong-he [24°80'N, 117°00'E]); Sheo-wu Co. (Yan-shan [27°30'N, 117°30'E]); Chong-an Co. (San-gang [27°70'N, 117°70'E]). **Jiangxi Prov.:** Hong-shan [?], alt. 950 m. **Guangdong Prov.:** Lian-xian Co. (Yao-an [24°70'N, 112°30'E]); Lo-chang Co. (Tian-tang [25°10'N, 113°30'E]); Shi-xing Co.

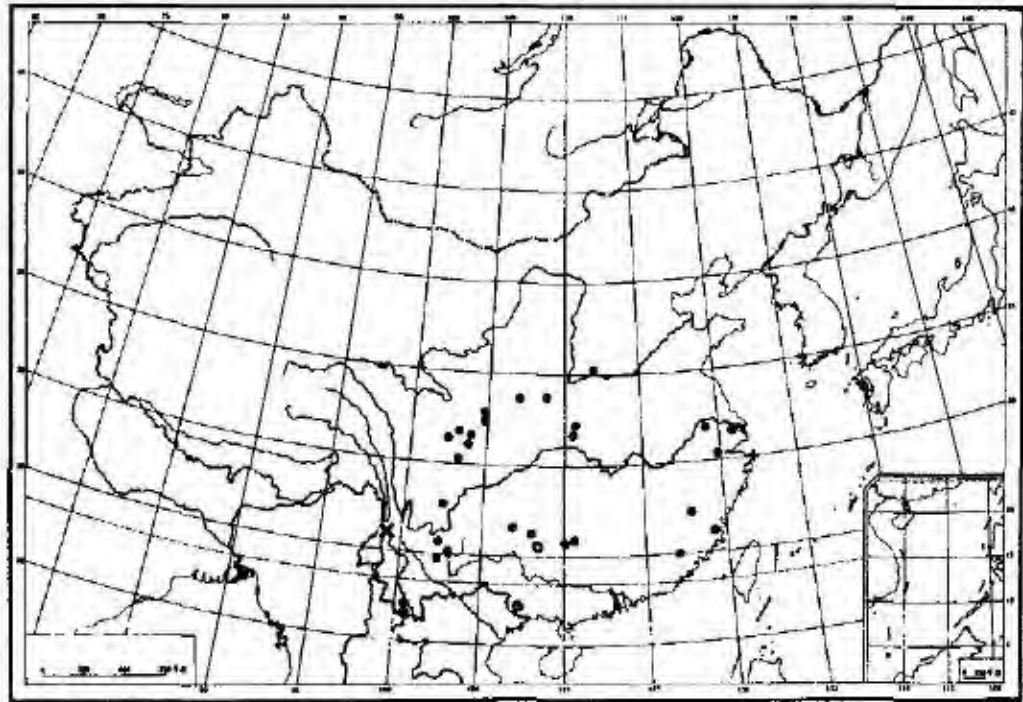


Fig. 2. Distribution of *Maltus* spp. in China. ● - *M. sinicus* Štys, ◆ - *M. elongatus* Štys, ✱ - *M. similis* Štys.

(Che-ba-ling [24°30'N, 114°30'E]). **Guangxi Prov.:** Long-sheng Co. (Hong-tan [25°60'N, 109°30'E]); Shang-lin Co. [23°40'N, 108°50']; Long-zhou Co. (Mt. Da-qing [22°30'N, 106°70'E]). **Guizhou Prov.:** Mt. Lei-gong [26°40'N, 108°20'E]). **Yunnan Prov.:** Bao-shan Co. [25°10'N, 99°10'E]; Lu-xi Co. [24°40'N, 98°50'E]; Jin-ping Co. (Da-meng-long [21°50'N, 100°60'E]), Meng-hun [21°30'N, 100°30'E], Meng-a [22°10'N, 100°20']; Meng-la Co. (Meng-la [21°40'N, 101°50'E], Shang-yong [21°20'N, 101°70'E]); Rui-li Co. (Meng-xu [24°00'N, 97°80'E]).

***Malcus flavidipes* Stål, 1859**

(Fig. 4)

MATERIAL. **Hainan Prov.:** Le-dong Co. (Mt. Jian-feng-ling [18°40'N, 108°30'E]); Bao-lin Co. [18°60'N, 109°70'E]; Wan-ning Co. (Xing-long [18°70'N, 110°10'E]); Qiong-zhong Co. [19°00'N, 109°80'E], Mt. Wu-zhi [18°80'N, 109°50'E]; Zhan-xian Co. [19°60'N, 109°60'E], Lin-gao Co. [19°30'N, 109°60'E]. **Guangxi Prov.:** Gui-lin City [25°20'N, 110°20'E]; Shang-lin Co. [23°40'N, 108°50'E]; Long-zhou Co. (Mt. Da-qing [22°30'N, 106°70'E]); Ping-xiang Co. [22°10'N, 106°70'E]. **Guizhou Prov.:** Luo-dian Co. [25°40'N, 106°70'E]. **Yunnan Prov.:** Lu-xi Co. [24°40'N, 98°50'E]; Rui-li Co. (Nong-dao [23°30'N, 97°60'E]); Jing-hong Co. (Jing-hong [22°00'N, 100°80'E], Da-meng-long [21°50'N, 100°60'E], Meng-yang [22°00'N, 100°80'E], Gan-lan-ba [22°40'N, 100°60'E]; Meng-hai Co. (Meng-bai [21°30'N, 100°40'E]; Meng-la Co. (Meng-la [21°40'N, 101°50'E]).

***Malcus furcatus* Stys, 1967**

(Fig. 5)

MATERIAL. **Yunnan Prov.:** Geng-ma Co. [23°50'N, 99°40'E]; Zheng-kang Co. [23°00'N, 99°00']; Jing-hong Co. (Da-meng-long [21°50'N, 100°60'E]); Ping-bian Co. (Mt. Da-wei, alt. 1800 m [22°50'N, 103°70'E]); Lü-chun Co., alt. 1900 m [23°00'N, 102°40'E]; Yong-ping Co., alt. 2300 m [25°60'N, 99°30'E].

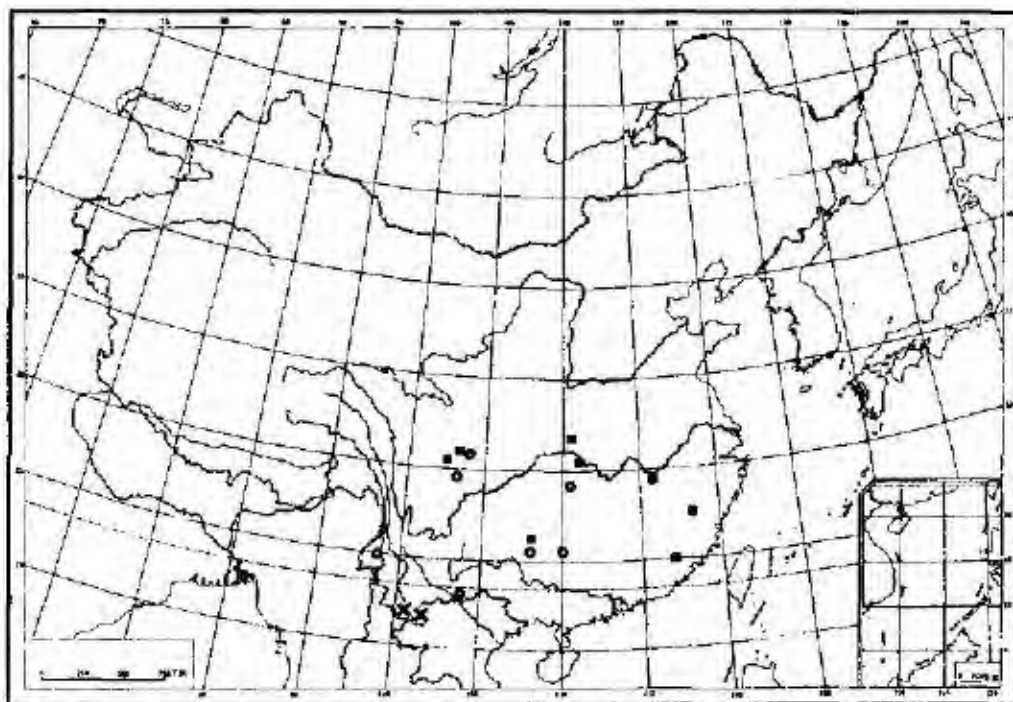


Fig. 3. Distribution of *Malcus* spp. in China. ■ — *M. denticulatus* Stys, ● — *M. auriculatus* Stys, * — *M. dentatus* Stys.

***Malcus gibbus* Zheng, Zou et Hsiao, 1979**
(Fig. 1)

MATERIAL. Yunnan Prov.: Si-mao Co. (near Si-mao City [22°70'N, 100°90'E]).

***Malcus idoneus* Horváth, 1914**
(Fig. 4)

MATERIAL. Taiwan Prov.: [see Horváth (1914) and Štys (1967)]. Yunnan Prov.: Jing-hong Co. (Da-meng-long [21°50'N, 100°60'E], Meng-song, alt. 1600 m [21°50'N, 100°40'E]); Meng-hai Co. (Meng-a [22°10'N, 100°20']); Ping-bian Co. (Mt. Da-wei, alt 1800 m [22°90'N, 103°70'E]); Lü-chun Co. [22°90'N, 102°60'E]. Xizang Autonom. Region: Zham Co., 1800 m [27°90'N, 85°90'E].

NOTE. The Sichuan (Mt. Omei) record of *M. idoneus* mentioned by Zheng & Zou (1981a) represents possibly an undescribed species.

***Malcus inconspicuus* Štys, 1967**
(Fig. 5)

MATERIAL. Hubei Prov.: Chang-yang Co. [30°40'N, 111°10'E]; Ba-dong Co. (Ba-dong [31°00'N, 110°30'E]). Jiangxi Prov.: Xing-zi Co. [29°40'E, 116°00'E]. Guangdong Prov.: Lian-xian Co. (Yao-an [24°70'N,

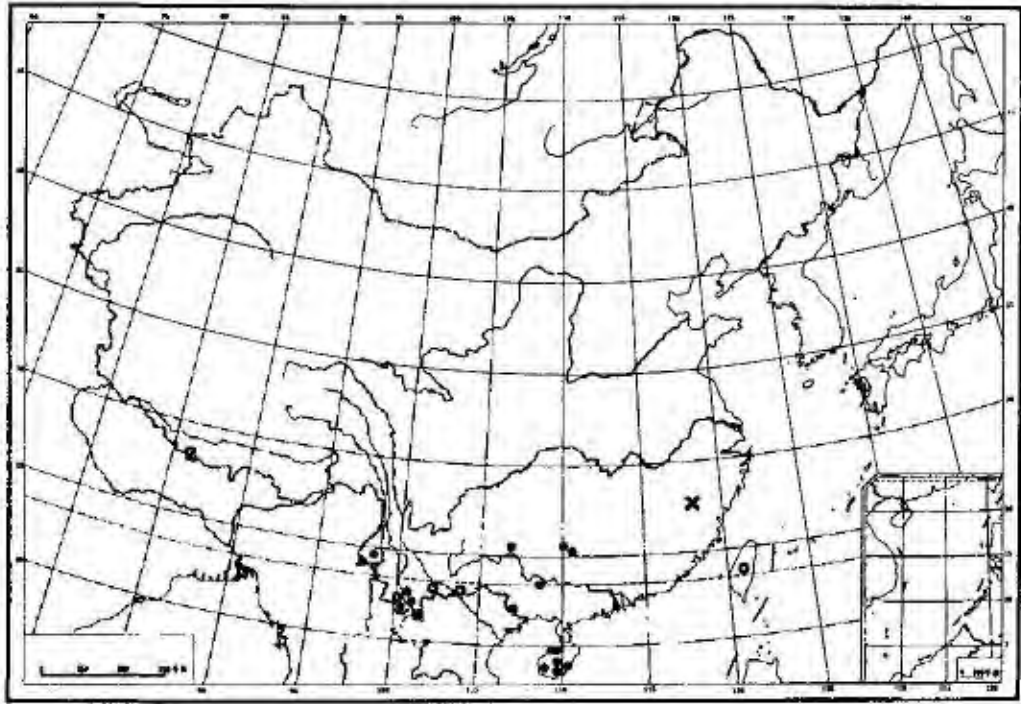


Fig. 4. Distribution of *Malcus* spp. in China. ● — *M. flavipes* Stål, ○ — *M. idoneus* Horváth, x — *M. japonicus* Ishikara & Hasegawa.

112°30'E]; Shixing Co. (Che-bu-ling [24°80'N, 114°30'E]) Guangxi Prov.: Guilin Co. (Guilin [25°20'N, 110°20'E]), Yangshuo Co. (Yangshuo [24°70'N, 110°40'E]); Longsheng Co. (Seu-men [25°70'N, 109°80'E]), Sing-an Co. (Mc Miao-er: Hua-jiang [25°90'N, 110°40']). Hainan Prov.: Lin-gao Co. [19°90'N, 109°60'E]. Guizhou Prov.: Li-bo Co. (Mao-lan [25°30'N, 108°00'E]), Luo-dian Co. [25°40'N, 106°70'E].

NOTE. Štys (1967) recorded two females from locality "China, Kwantung, Tungbing (= Haining) [21°35'N, 107°57'E]." The latitude and longitude are located in Vietnam after present map, while "Haining", noted by Štys (1967), is a city in Zhejiang Province in eastern China [30°50'N, 120°70'E].

Malcus indicus Štys, 1967
(Fig. 6)

MATERIAL. Yunnan Prov.: Jing-hong Co. (Meng-long: Man-bing, alt 750 m [21°50'N, 100°60'E]); Meng-hai Co. (Meng-hun [21°80'N, 100°30'E]).

Malcus insularis Štys, 1967
(Fig. 1)

MATERIAL. Taiwan Prov. [see Štys (1967)]

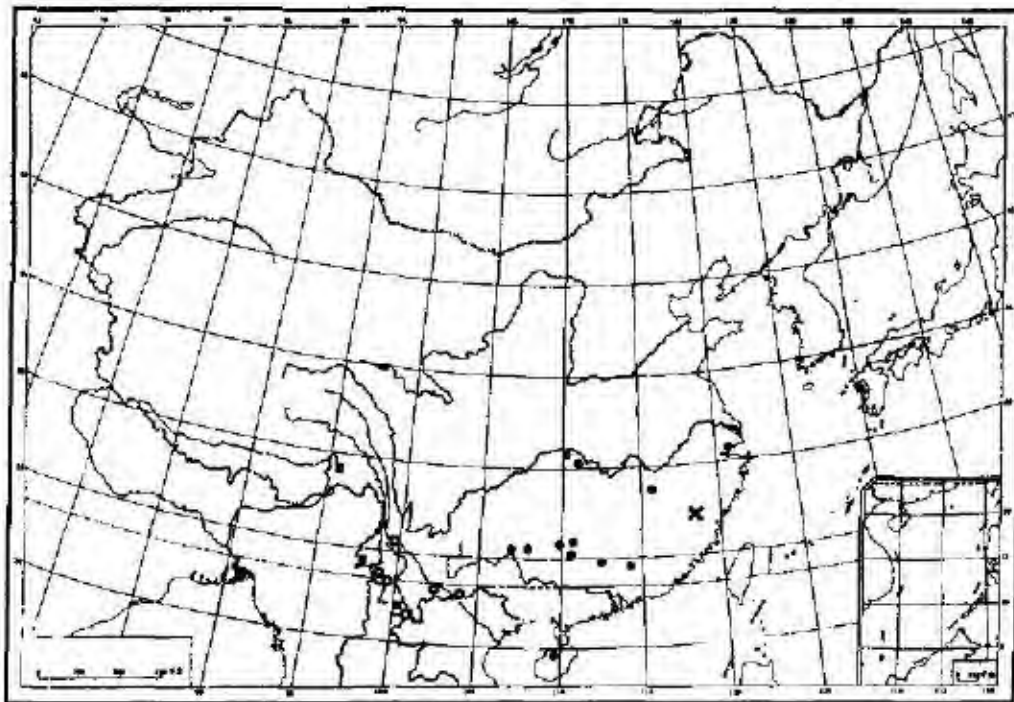


Fig. 5 Distribution of *Malcus* spp. in China. ● - *M. inconspicuus* Štys, ○ - *M. furcatus* Štys, ■ - *M. subauriculatus* Zheng, Zou et Hsiao, ✕ - *M. arcuatus* Zheng, Zou et Hsiao.

***Malcus japonicus* Ishihara et Hasegawa, 1941**
(Fig. 4)

MATERIAL. Fujian Prov.: Chong-an Co. (San-gang [27°70'N, 117°70']).

***Malcus nigrescens* Štys, 1967**
(Fig. 1)

MATERIAL. Hainan Prov.: Mt. Diao-luo [18°70'N, 109°80']. Gulzhou Prov.: Li-bo Co. (Mao-lan [25°40'N, 107°80']). Xizang Autonom. Region: Medog Co. [29°20'N, 95°30'E].

***Malcus noduliferus* Zheng, Zou et Hsiao, 1979**
(Fig. 6)

MATERIAL. Guangdong Prov.: ("Yao-shan" [25°20'N, 113°20']). Yunnan Prov.: Bao-shan Co. [25°10'N, 99°10']; Lu-xi Co. [24°40'N, 98°50'E]; Jing-hong Co. (Da-meng-long [21°50'N, 100°20'E]); Meng-ha Co. (Meng-a [22°10'N, 100°20'E]).

***Malcus piceus* Zheng, Zou et Hsiao, 1979**
(Fig. 6)

MATERIAL. Guangxi Prov.: Long-sheng Co. (Hong-tan [25°70'N, 110°00'E]). Xizang Autonom. Region: Zham Co. (Zham, alt. 1800 m, and You-yi-qiao [27°90'N, 85°90']).

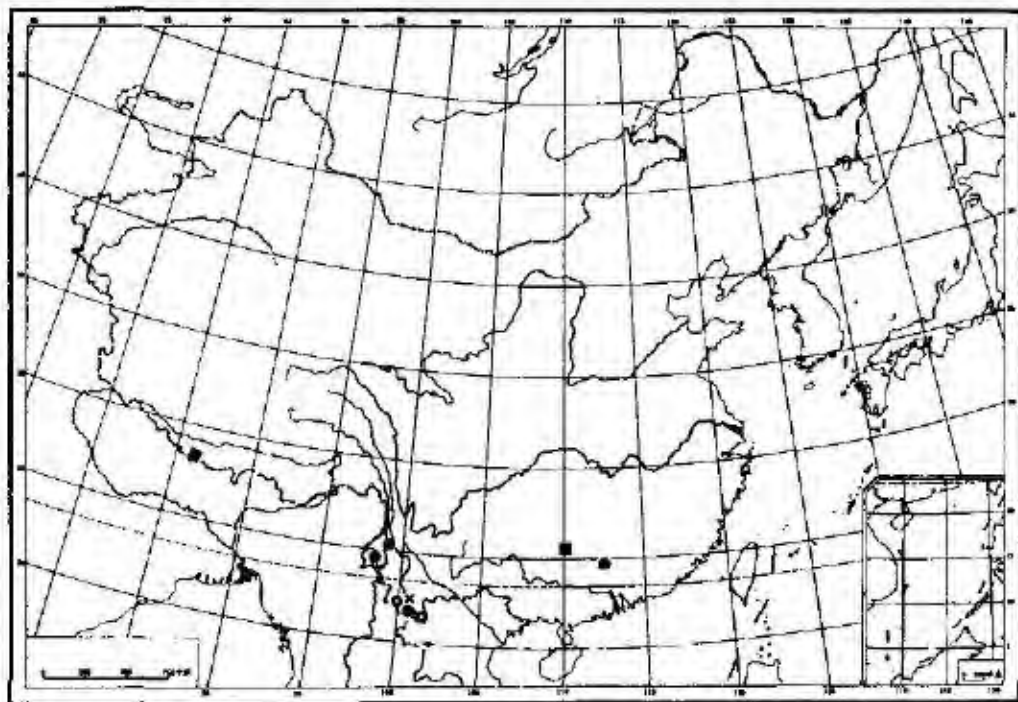


Fig. 6. Distribution of *Malcus* spp. in China. ● — *M. noduliferus* Zheng, Zou et Hsiao, ◐ — *M. setosus* Štys, ■ — *M. piceus* Zheng, Zou & Hsiao, * — *M. indicus* Štys.

***Malcus setosus* Štys, 1967**

(Fig. 6)

MATERIAL Yunnan Prov.: Jing-hong Co. (Jing-hong [22°00'N, 100°30'E], Da-meng-long [21°50'N, 100°60'E]), Meng-la Co. (Meng-la [21°40'N, 101°30'E], Shang-yong [21°20'N, 101°70'E])

***Malcus similis* Štys, 1967**

(Fig. 2)

MATERIAL Yunnan Prov.: Lu-shui Co. [25°00'N, 98°30'E]

***Malcus sinicus* Štys, 1967**

(Fig. 2)

MATERIAL Shanai Prov.: Yuan-qu Co. [35°30'N, 111°70'E] Gansu Prov.: Wen-xian Co. (Fan-ba, alt. 880 m [32°30'N, 105°00'E]) Shaanxi Prov.: Qin-ling Railway Station [34°30'N, 106°30'E], Chang-an Co. (Wei-zhi-ping [33°30'N, 108°30'E]) Jiangsu Prov.: Nanjing (= Nanking in Štys (1967), Suzhou (= Soochow in Štys (1967)) Zhejiang Prov.: Mi Tian-mu [30°40'N, 119°30'E] Hubei Prov.: Fang-xian Co. (Qiao-shang [31°30'N, 110°70'E], Mt. Sheng-nong-jia Song-bai, alt. 700 m [31°70'N, 110°60'E]) Fujian Prov.: Fuzhou (Gu-shan [26°00'N, 119°30'E]), Jian-yang Co. [27°30'N, 118°10'E], Long-yan Co. [25°10'N, 117°00'E], Cheng-an Co. (San-gang [27°70'N, 117°70'E]) Sichuan Prov.: Pingwu Co. ("Khotzigen" [32°38'N, 104°34'E] — type locality [Štys (1967)], Mt. Qing-cheng, alt. 960 m [30°30'N, 103°50'E]), Mao-wen Co. (Feng-yi, alt. 1900 m [31°60'N, 103°30'E]), Guan-xian Co. (Er wang-miao, alt. 750–800 m [31°00'N, 103°60'E]), Bao-xing Co. (Bao-xing, alt. 750–1350 m [30°30'N, 102°30'E]), Qiao-qu, alt. 2400 m [30°70'N, 102°70'E]), Xi-chang Co. (Xi-chang [27°30'N, 102°20'E]), "River Sjaoczi-kho between villages Pan'sha-myrt and Sin-chan-czy" (the locality at the vicinity of Fubian [31°20'N, 102°40'E] in Xiao-jin Co. in the present map (according to Komarov 1928) represents very probably the locality mentioned by Štys (1967)) Guangdong Prov.: Le-chang Co. (Tian-tang [25°10'N, 113°30'E]) Guangxi Prov.: Long-sheng Co. (Cu-jiang [25°70'N, 100°00'E]), Xing-an Co. (Mt. Miao-cr, alt. 1000–2300 m [25°30'N, 110°40'E]) Guizhou Prov.: Guiyang [26°60'N, 106°70'E], Mt. Lei-gong [24°40'N, 108°20'E] Yunnan Prov.: Kunming (Xi-shan [25°00'N, 102°70'E]), An-ning Co. (Wen-quan [24°30'N, 102°40'E]), Wuding Co. (Shi-zhi-shan [25°50'N, 102°30'E]), Jing-hong Co. (Meng-song, alt. 1600 m [21°50'N, 100°40'E]), Meng-hai Co. (Meng-a Meng-kang [22°10'N, 100°30'N])

***Malcus subauriculatus* Zheng, Zou et Hsiao, 1979**

(Fig. 5)

MATERIAL Yunnan Prov.: Men-lai Co. (Meng-a [22°10'N, 100°30'E]), Rui-li Co. (Meng-xiu [24°00'N, 97°30'E]) Xizang Auton. Region: Medog Co. [29°20'N, 95°30'E]

DESCRIPTION OF PHALLIC STRUCTURES

Phall. of the six species studied posses very similar structure, commonly fit very well the Štys's (1967) description of the genus *Malcus*

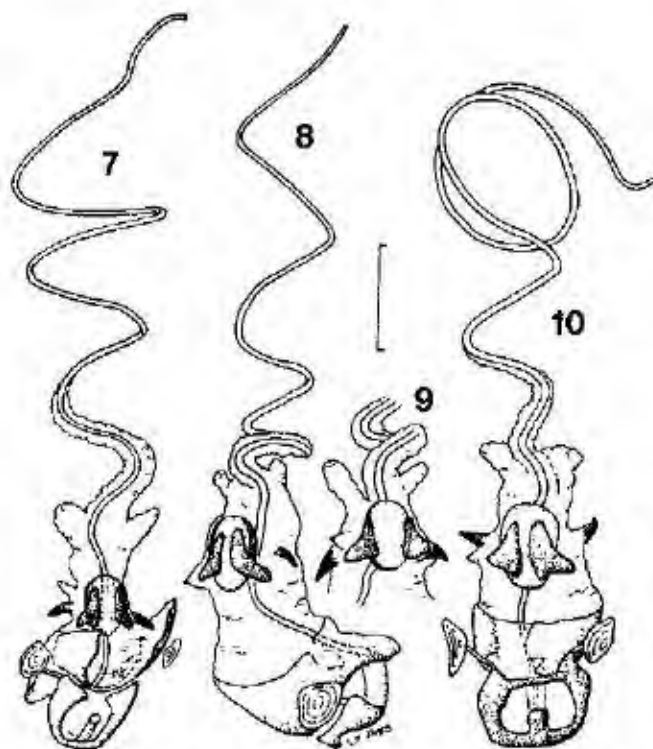
The partly sclerotized phallotheca (Figs 8, 11, pht) of shape of shallow bowl or deep disc, in the deflated state, endosoma sinking in, anteromedial wall of phallotheca desclerotized, dividing anterior area of phallotheca into two sclerotized, anterolateral parts, protruding from outline anterodorsad in form of a pair of triangular plates or processes (Figs 7, 11, 12, php), corresponding with Štys's (1967) "lateral processes of phallotheca". Shape of inflated phallotheca completely changes to short barrel, above mentioned configuration changes consequently, the processes-like anterolateral parts of the phallotheca are turned into mediadorsad position, not protruding from outline any more (Figs 8, 10, php). Therefore, it seems probable that these "phallothecal processes" in Malcidae are not homologous with the proper lateral processes found in phallotheca of Lygaeinae and some other subfamilies of Lygaeidae (Ashlock 1957, Štys 1967)

Two pairs of endosomal sclerotized processes laterally (Figs 7, 9–12, ep), at the level of sperm reservoir (Figs 10, 12, sr), characteristic for the genus *Malcus*. The processes are probably directed proximal, or ventral, when phallus fully inflated (Figs 8, 9), anchoring it inside the female genital chamber during “in copula” state. Pair of apical, undivided, membranous endosomal lobes (Figs 7, 8, 10–12, el) developed, right lobe larger and more stouter than narrow left lobe, pointing more laterad. A possibility that this structure represents “basal vesical membranous lobe” also exists.

Two pairs of endosomal processes at distal part of phallus are also developed in the genus *Berytinus* (Berytidae; Berytinae; Péricart 1984), reminding somewhat the general scheme found in *Malcus*, but the processes are membranous in *Berytinus*.

The proximal part of gonoporal process (Fig. 7, gp) is surrounded by membranous tube, tapering distad. Any helicoid process was not found in *Malcus*, as Štys (1967) correctly emphasized. Henry (1997) used state “helicoid process presented”, based on Ashlock’s (1957) description, as one of the synapomorphies supporting the monophyly of the family Malcidae. This statement is true only for the malcids subfamily Chauliopininae (Sweet & Schaefer 1985, Zheng unpubl.).

Six species examined can be segregated into two groups after state of phallic structures, the first: *M. dentatus*, *M. elongatus*, *M. furcatus*, and *M. setosus*, the second: *M. flavidipes* and *M. sinicus*. The differences between the groups are as follows:



Figs. 7–10. Phallus of *Malcus* spp. 7 – *M. dentatus* Štys; 8–9 – *M. elongatus* Štys. 10 – *M. setosus* Štys. Scale bar = 0.13 mm

a) There is a small membranous lobe just at anterior, or ventral side of the right endosomal sclerotized process in *M. dentatus*, *M. elongatus*, *M. furcatus*, and *M. setosus*. The lobe is small, smaller than the sclerotized process, heavily narrowed into sharp apex. Any such lobe was not found in the second *Malcus* group.

b) The size of the phallic body is slightly larger, and the gonoporal process is conspicuously longer in *M. flavidipes* and *M. sinicus* (Figs 11, 12), in comparison with the first *Malcus* group. The size and length is not distinctly in proportion with short body of two species mentioned.

c) The mediobasal apex of sclerotized part of lateral wall of phallosome is sharper and more produced in *M. flavidipes* and *M. sinicus* than in the first *Malcus* group.

However, the differences in phallic structures among members of each *Malcus* group are relatively small. Phalli of *M. dentatus*, *M. elongatus*, *M. furcatus*, and *M. setosus* are with difficulty distinguishable each from other, despite of great somatic differences among the species. In the other *Malcus* group, *M. sinicus* is distinguishable after slightly broader right apical membranous lobe of endosoma than in *M. flavidipes*.

Since all the conclusions mentioned above are based mostly on only partly inflated phalli, their reliability need to be ascertained by the next study of fully inflated phalli.

BIOLOGICAL NOTES

The *Malcus* species are usually found in the sunny forest margins and clearings, sometimes in road sides, around villages and orchards. We never can meet with them inside the thick subtropical forests, only with a dim light. Most of the specimens were collected from a herbaceous vegetation, only rarely were found on shrubs and trees.

The adults of the species observed by author usually inhabit both surfaces of leaves, freely moving in moderate speed. They do not exhibit any type of mimicry or protective colour pattern, as the brown colour usually contrasts well with the green background. The bugs run jerkily when disturbed, but not so nimbly and quickly as the rhyarochromine lygaeids. Although more individuals were sometimes found on one leaf, they are usually dispersed and no tendency toward aggregation is exhibited, as in some tingids. No bug tried ever to fly, when was disturbed or even touched. Both nymphs and adults were sometimes found together on one leaf.

The leaves, on which the *Malcus* individuals were found, are usually scattered with whitish chlorotic spottings (similar to those caused by cicadellids or tingids), possibly caused by the feeding of the bugs.

The author collected the adults of *Malcus flavidipes* repeatedly, in Jian-feng-ling in the Hainan Island, from leaves of the following Convolvulaceae plants: *Merremia* sp. (with nymphs), *Ipomoea nil* (L.) Choisy, *I. batatas* (L.) Lam. (with nymphs) and *Ipomoea* sp. The other foodplant of *Malcus flavidipes* would be *Kleinhovia hospita* L., a wood plant of Sterculiaceae; only adults were found on the leaves of young shoots sprouting from the ground. Adults of *Malcus flavidipes* were found also on *Humulus scandens* (Lour.) Merr. (Moraceae) in south-west Yunnan (Meng-la).

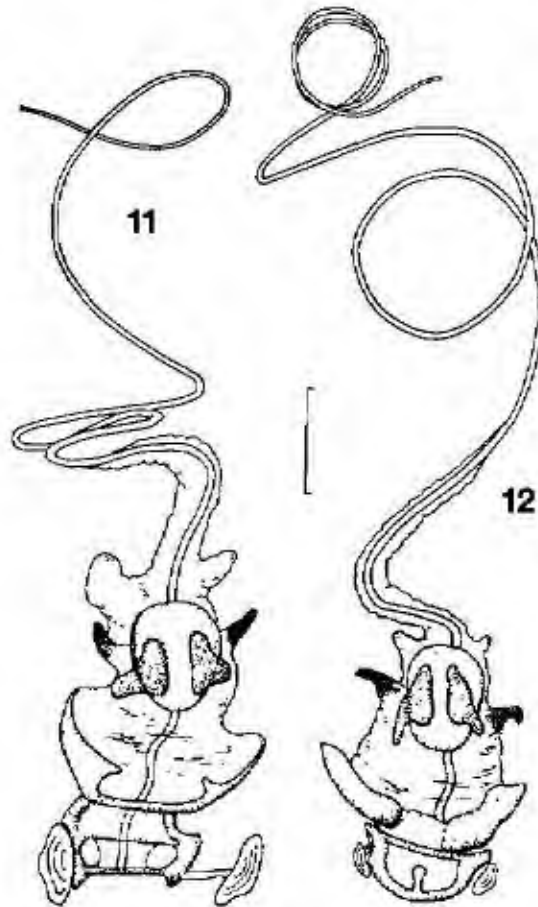
Malcus sinicus is a common species, widely distributed in China. The adults and nymphs were collected by the author on *Humulus scandens* (Gansu Prov.: Wen-xian), *Phaseolus vulgaris* L., and *Pueraria* sp. (Leguminosae) (Yunnan Prov.: Wu-ding).

The following plants were discovered as foodplants of *Malcus inconspicuus*: *Boerhaavia nivea* (L.) Gaud. (Urticaceae) (Guangxi prov.: Mt. Miao-er, collected by the author; Jiangxi Prov.: Xin-zhi, and Hubei Prov.: Chang-yang, noted on labels of specimens sent to the author for identification), *Cucurbita moschata* (Duch.) Poir. (Cucurbitaceae) (Hubei Prov.: Chang-yang, noted by the collector C.-r. Li; Guangdong Prov.: Liang-xian, adults and nymphs collected by the author), *Gly-*

cine max (L.) Merr. (Fabaceae) (Guangdong Prov.: Liang-xian, only one adult, collected by the author), *Alocasia* sp. (Araceae) (adults and one nymph on undersurface of leaves, Guizhou Prov.: Li-bo, noted by the collector C.-j. Ma). The adults of *Malcus elongatus* were found together with the nymphs on *Pueraria* sp. by the author in Guangdong Prov.: Shi-xing.

A series of *Malcus furcatus* was found by the author on the leaves of *Girardinia* sp. (Urticaceae), a plant with poisonous hairs on its leaves (with strong stinging effect when touched), in south Yunnan Prov.: Lü-chun.

The above data show that the list of foodplants of *Malcus* species includes, in the present, representatives from the following families: Araceae, Convolvulaceae, Fabaceae, Moraceae, Sterculiaceae, and Urticaceae; Musaceae (including the banana tree) should be added according to Štys (1967). The genus *Malcus* seems to be more closely associated with, at least, the four first men-



Figs 11, 12. Phyllus of *Malcus* spp., anterior view, 11 - *M. sinicus* Štys 12 - *M. flavidus* Stål. Scale bar = 0.13 mm.

tioned families, from which Urticaceae and Moraceae are closely related groups. *Malcus japonicus* was recorded from *Morus bombycis*, wood plant also from Moraceae (Štys 1967). The Fabaceae plants are also commonly fed by *Chauliops* spp. (Chauliopiniae), therefore they might have a strong association with the whole family Malcidae.

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Comparative and developmental morphology of the forewing color pattern in Pyrrhocoridae (Hemiptera)

Jan ZRZAVÝ

Department of Zoology of the Faculty of Biological Sciences, and Institute of Entomology, Branišovská 31,
CZ-370 05 České Budějovice, Czech Republic

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Abstract. Postembryonic development of forewing color patterns of two model species, *Pyrrhocoris apterus* (Linnaeus, 1758) and *Dysdercus virgatus* (Fabricius, 1775) (Hemiptera: Pyrrhocoridae), is analysed with the aim of revealing developmental-morphological regularities involved in color-pattern organization. This analysis is supplemented with a comparative study of diversity of color patterns among 82 species of the Pyrrhocoridae. Comparison of both approaches suggests that the pyrrhocorid forewing color patterns are formed by differential activity of seven prepattern centers and by differential melanization of four independent background areas.

Morphology, development, phylogeny, coloration, epidermis, cuticle

INTRODUCTION

The present paper follows up with the preceding studies analysing hemipteran, particularly pyrrhocorid coloration from both ecological (Zrzavý & Nedvěd 1997, 1999) and developmental perspectives (Zrzavý 1995), and is focused on the developmental-morphological organization of the forewing color patterns in Pyrrhocoridae. More general theoretical discussion of application of the parsimony (cladistic) methodology to ontogenetic questions will be published elsewhere.

Insect color patterns are intensely studied in butterflies, especially by H. F. Nijhout and his coworkers (for reviews see Nijhout 1991, 1994). Their project represents an exceptional synthesis of comparative morphology, developmental biology, and genetics, recently also with fascinating molecular developmental data appended (Carroll et al. 1994). The color patterns of pyrrhocorid bugs provide three important methodological advantages not seen in the butterflies (Zrzavý 1995): (a) their color patterns are not limited to single organs (like butterfly wings); (b) the bugs are hemimetabolous: their patterns are formed more continuously than the butterflies' ones, so that their analysis contains also an ontogenetic temporal component; (c) there are two independent patterns, epidermal pigmentation and cuticular melanization: their topological congruence may mark some more profound morphogenetic regularities which drive both patterns to codevelop and coevolve.

MATERIAL AND METHODS

Material for comparative morphology

Altogether 81 species of 32 genera of the Pyrrhocoridae (= 70% of generic diversity) were examined (see Table 1). Macropterous or brachypterous, but never micropterous morphs were selected for analysis. Some species [*Pyrrhocoris apterus* (Linnaeus, 1758), polymorphic *Dysdercus* spp., *Probergrothius sexpunctatus* Laporte, 1832] were studied on a large material to evaluate morphological regularities involved in their individual color-pattern variability. Unless otherwise stated, only adults were studied.

Material for developmental morphology

The model pyrrhocorid species, *Pyrrhocoris apterus*, was subjected to detailed morphological and ontogenetic analysis, using not only wildtype but also color mutations and strains, viz., *melanotic* (*m*), *white* (*w* = *wh*), *yellow* (*y* = *yw*), *Pale* (*Pa*), *Apricot* (*Ap*), *mosaic* (*mo*), *yolk body* (*yb*), *unstable micropterous* (*ump*), and *reddish lobes* (*rl*) [cf. (17)] (for reviews see Socha 1993, Sláma 1998).

Prothetelic specimens (with precocious appearance of imaginal characters in a larva or in a larval-adult intermediate), induced by JHA-treatment (Methoprene in acetone solution, 1 µg/µl, topical application), were used to reveal pattern-forming processes involved during metamorphosis of the model species [*P. apterus*, *Dysdercus cingulatus* (Fabricius, 1775)]. Course of postecdysial melanization was studied using specimens fixed in different stages of tanning (last larvae, adults).

Morphological analysis

Areas of larval wingpads were homologized with those of adult wings according to Štys' (1967) interpretation of forewing venation in the Pentatomomorpha (Fig. 1A). Future venation and fracture pattern is visible on wingpads of the 5th (last) instar larvae (*L*₅); it is usually distorted and nearly undistinguishable in prothetelic specimens.

Methodology of "reconstruction" of color-pattern organization was published in detail by Zrzavý (1995; cf. Nijhout 1991, 1994). Only those presumed pattern centers which are marked by a distinct spot in at least one specimen's forewing were used for the construction of a set of centers (Fig. 1C). The seven centers (*c1* to *c7*), the color pattern of any pyrrhocorid species may be homologized with, was used as a blueprint for analysis of individual color patterns (Table 1). Individual color patterns were coded "1" for active prepattern center, and "0" for inactive. Naturally, uniformly dark wings (or their parts) bear no information about prepattern centers' activity; these centers are then coded as "?".

Parsimony analysis of prepattern hierarchy

Diversity of the bug color patterns is considered here to be derived from a stable system of pattern-forming centers (the "prepattern"), so that is equivalent to diverse expression of *the same* prepattern (some prepattern centers remain inactive). The data matrix (prepattern centers vs. species) was analysed using standard parsimony methods, but in a transposed form (centers are grouped according to their co-activity in individual species). The current

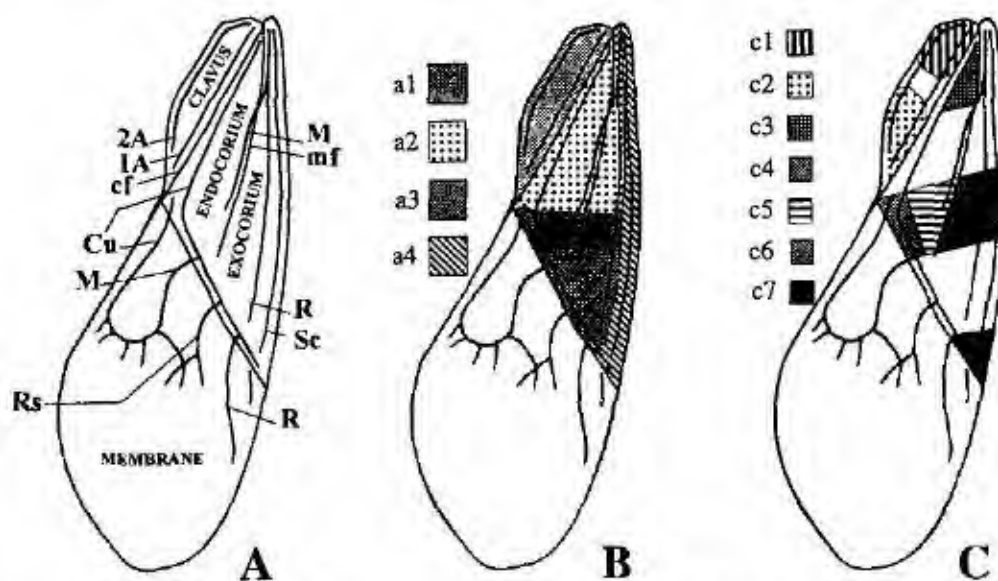


Fig. 1. Pyrrhocorid forewing: (A) Morphological terminology (*mf* – median fracture, *cf* – claval fracture, *Sc*, *R*, *M*, *Cu*, *1A*, and *2A* – wing veins). (B) Structure of background (*a1* to *a4*). (C) Structure of pattern (*c1* to *c7*). Orientation: proximal – above, distal – below, anterior – right, posterior – left.

Tab. 1. Expression of propattern centers in pyrrhocid genera and species

Genus/species	c1	c2	c3	c4	c5	c6	c7	No
Pyrrhocoridae Amyot et Serville, 1843	1	1	1	1	1	1	1	1
<i>Aderrhus flavipes</i> Stål, 1966	?	?	?	?	?	?	?	2
<i>Aeschines bucculatus</i> Stål, 1863	?	?	0	0	?	?	?	3
<i>Antiochus</i> Stål, 1863	0	1	0	1	1	1	1	4
<i>A. coqueberti</i> (Fabricius, 1784)	0	0	0	0	0	0	0	5
<i>A. lineatipes</i> Stål, 1858	0	1	0	1	1	1	1	6
<i>A. nigripes</i> (Burmeister, 1835)	0	0	0	0	0	0	0	7
<i>A. reflexus</i> Stål, 1863	?	?	?	?	?	?	?	8
<i>A. rufus</i> Stål, 1863	0	0	0	0	0	0	0	9
<i>Armatus orithocephaloides</i> (Brodin, 1912)	?	?	?	?	?	?	?	10
<i>Calliphagus longirostris</i> (Drury, 1782)	1	0	0	1	1	1	1	11
<i>Ctenops carinatus</i> (Fabricius, 1775)	0	0	0	0	0	0	0	12
<i>Dermatops erebus</i> Distant, 1909	?	?	?	?	?	?	?	13
<i>Dindymus</i> Stål, 1861	0	0	0	1	1	1	1	14
<i>D. bicolor</i> Herrich-Schaeffer, 1784	0	0	0	0	0	0	0	15
<i>D. flavipennis</i> Blute, 1931	?	?	?	?	?	?	?	16
<i>D. versicolor</i> (Herrich-Schaeffer, 1850)	?	?	0	0	0	0	?	17
<i>Dynamenus venustus</i> (Walker, 1873)	?	?	?	1	1	1	1	18
<i>Dysdercus</i> Guérin Méneville, 1831	0	1	0	1	1	1	?	19
<i>D. (Dysdercus) Guérin Méneville, 1831</i>	0	1	0	1	1	1	1	20
<i>D. (D.) albofasciatus</i> Berg, 1878	?	?	?	1	1	1	1	21
<i>D. (D.) andreae</i> (Linnaeus, 1758)	?	?	0	1	1	P	1	22
<i>D. (D.) cardinalis</i> Gerstaecker, 1873	0	0	0	1	1	?	?	23
<i>D. (D.) cingulatus</i> (Fabricius, 1775)	0	0	0	0	1	1	P	24
<i>D. (D.) concinnus</i> Stål, 1861	0	0	0	0	1	1	0	25
<i>D. (D.) fasciatus</i> Signoret, 1861	0	0	0	P	1	?	?	26
<i>D. (D.) flavidus</i> Signoret, 1861	0	0	0	1	0	0	0	27
<i>D. (D.) jamaicensis</i> Walker, 1872	0	1	0	P	1	1	1	28
<i>D. (D.) longirostris</i> Stål, 1861	0	0	0	0	0	0	0	29
<i>D. (D.) melanoderes</i> Karsch, 1892	0	0	0	0	0	0	0	30
<i>D. (D.) mimus</i> Hussey, 1929	?	?	?	?	?	?	?	31
<i>D. (D.) mimus</i> Say, 1832	0	0	0	0	0	0	0	32
<i>D. (D.) nigrofasciatus</i> Stål, 1855	0	0	0	P	1	1	P	33
<i>D. (D.) obscuratus</i> Distant, 1883	?	?	?	?	?	?	?	34
<i>D. (D.) ruficeps</i> (Perty, 1833)	?	?	?	?	?	?	?	35
<i>D. (D.) ruficollis</i> (Linnaeus, 1764)	0	0	0	P	P	P	P	36
<i>D. (D.) sanguinarius</i> Stål, 1870	0	1	0	0	1	1	1	37
<i>D. (D.) superstiosus</i> (Fabricius, 1775)	0	0	0	1	1	P	1	38
<i>D. (D.) suturalis</i> (Herrich-Schaeffer, 1842)	?	?	?	?	?	?	?	39
<i>D. (Neodysdercus) Stål, 1965</i>	0	0	0	1	1	1	0	40
<i>D. (N.) intermedius</i> Distant, 1902	0	0	0	1	1	1	0	41
<i>D. (N.) pretiosus</i> Distant, 1902	0	0	0	1	1	1	0	42
<i>D. (Paradysdercus) Stål, 1965</i>	0	1	0	1	1	1	1	43
<i>D. (P.) evanescens</i> Distant, 1902	0	0	0	0	0	1	0	44
<i>D. (P.) festinus</i> Gerstaecker, 1892	0	0	0	1	1	1	0	45
<i>D. (P.) kuanu</i> (Fabricius, 1775)	0	0	0	1	1	1	P	46
<i>D. (P.) poecilus</i> (Herrich-Schaeffer, 1843)	0	1	0	1	1	?	?	47
<i>D. (P.) solenis</i> (Herrich-Schaeffer, 1843)	0	0	0	0	1	1	0	48
<i>D. (Megadysdercus) mestostigma</i> Distant, 1888	0	0	0	0	0	0	0	49
<i>Ectatops</i> Amyot et Serville, 1843	0	0	0	0	0	0	0	50
<i>E. fuscus</i> Stål, 1863	?	?	?	?	?	?	?	51
<i>E. ophthalmicus</i> (Burmeister, 1835)	0	0	0	0	0	0	0	52
<i>E. seminiger</i> Stål, 1863	?	?	?	0	0	0	0	53
<i>Euscopus</i> Stål, 1870	0	0	0	1	1	1	1	54

Tab. 1. Continued

<i>E. albatrus</i> Distant, 1909	?	?	0	1	1	1	1	55
<i>E. rufipes</i> Stål, 1870	?	?	0	0	1	1	1	56
<i>Gromerus ruficeps</i> Villiers, 1951	0	0	0	0	0	0	0	57
<i>Lodotiana aegyptius</i> (Linnaeus, 1758)	?	?	0	0	1	1	?	58
<i>Melamphaus</i> Stål, 1868	0	0	0	1	1	1	1	59
<i>M. faber</i> (Fabricius, 1787)	?	?	?	1	1	1	1	60
<i>M. fulvomarginatus</i> (Dohrn, 1860)	?	?	?	?	?	?	?	61
<i>Neodindymus migratorius</i> (Distant, 1903)	?	?	?	0	?	?	?	62
<i>Obstetricella abortiva</i> (Gerstaecker, 1873)	?	?	?	?	?	?	?	63
<i>Paradindymus</i>								
<i>madagascariensis</i> (Blanchard, 1849)	?	?	?	1	1	1	1	64
<i>Paraetiatops costalis</i> (Walker, 1873)	0	0	0	0	0	0	0	65
<i>Probergrothius</i> Kirkaldy, 1904	1	0	0	0	1	1	1	66
<i>P. exsanguis</i> (Gerstaecker, 1892)	1	0	0	0	0	0	1	67
<i>P. nigricornis</i> Stål, 1861	P	0	0	0	0	0	1	68
<i>P. notabilis</i> Distant, 1902	1	0	0	0	0	0	1	69
<i>P. sanguinolens</i> Amyot et Serville, 1843	1	0	0	0	0	0	0	70
<i>P. scutellarius</i> Walker, 1872	0	0	0	0	1	0	1	71
<i>P. sexpunctatus</i> Laporte, 1832	1	0	0	0	1	1	P	72
<i>Pseudindra verrucosa</i> (Distant, 1908)	?	?	?	?	?	?	?	73
<i>Pyrrhocoris</i> Fallén, 1814	0	0	1	0	1	1	0	74
<i>P. apterus</i> (Linnaeus, 1758)	?	?	1	0	1	1	?	75
<i>P. fieberti</i> Kuschakevich, 1867	?	?	?	?	?	?	?	76
<i>P. juscopunctatus</i> Stål, 1858	?	?	?	?	?	?	?	77
<i>P. marginalis</i> (Koloni, 1845)	?	?	?	?	?	?	?	78
<i>P. niger</i> Reuter, 1888	?	?	?	?	?	?	?	79
<i>P. sibiricus</i> Kuschakevich, 1867	?	?	?	?	?	?	?	80
<i>P. tibialis</i> Stål, 1874	0	0	P	0	P	0	0	81
<i>Pyrrhophelus posthumus</i> Horvath, 1892	0	0	0	0	1	1	0	82
<i>Roscius guilhelmi</i> Bergroth, 1926	0	1	?	1	1	1	1	83
<i>Saldoides ornatus</i> Breddin, 1901	?	?	?	?	?	?	?	84
<i>Scantius</i> Stål, 1866	0	0	0	0	0	0	0	85
<i>S. andriai</i> Cachan, 1952	?	?	?	?	?	?	?	86
<i>S. forsteri</i> (Fabricius, 1781)	?	?	?	P?	?	?	P?	87
<i>S. nervosus</i> (Cachan, 1952)	?	?	?	?	?	?	?	88
<i>Sericocoris</i> Karsch, 1892	1	0	0	0	0	0	0	89
<i>S. avromelanthos</i> Karsch, 1892	0	0	0	0	0	0	0	90
<i>S. furidus</i> (Reuter, 1882)	1	0	0	0	0	0	0	91
<i>Stanga variegata</i> Blöte, 1933	?	?	?	0	1	1	1	92
<i>Stenatus circumcinctus</i> (Lethierry, 1883)	?	?	?	1	1	1	1	93
<i>Stictaulax circumsepta</i> Stål, 1870	0	0	0	0	0	0	0	94
<i>Syncretus mudanganus</i> Ghauri, 1972	?	?	?	0	?	?	?	95

Generic and subgeneric names are boldfaced, *c1* to *c7*—propattern centers (Fig. 1C), No—number of a column in Table 2; 1—present, P—present in some individuals, 0—absent, ?—probably present (in species with uniformly dark wings or their parts), P?—probably present in some individual.

Linnean classification was used as possible approximation of the cladogram in an attempt to deal with the lacking phylogenetic analysis of the Pyrrhocondae (Schaefer 1993). Only three hierarchical levels, family, genera, and species, were used assuming that pyrrhocond genera are mostly monophyletic, well-established. *Dysdercus* subgenera were used as well (Table 1). The putative "common ancestors of genera" were coded as "1" if at least one congeneric species was "1". The same method was used for coding the subgenera and the family as a whole. Genera and subgenera represented by a single species in this analysis were coded only once, as species. Each center was therefore coded as either "1", or "0", or "?" in 81 species, in 13 "ancestors" of genera/subgenera, and in an "ancestor" of the family as a whole, i.e. in 95 taxonomic units (Table 2). This dataset was analysed by Hennig86 (Version 1.5; option /e*).

Tab. 2 Matrix listing the distribution of prepattern centers among pyrrhocorid species, subgenera, genera, and a family (sequence of columns corresponds to the sequence of taxa in Table 1)

No	000000000111111111222222222233333333334
	1234567890123456789012345678901234567890
c1	1220000202102002220022000000002002200020
c2	1221010202602002221122000001002002201020
c3	1200000202002002020020000000002002200020
c4	1201010202102102011111100111002012210121
c5	121101020210210201111111101002012211121
c6	1211010202102102011111111101002012211121
c7	1211010002102100211111210201000012211120
No	44444444455555555555666666666677777777778
	1234567890123456789012345678901234567890
c1	000000000002020220202222011111012022222
c2	0001000100020202202022222000000002022222
c3	0000000000020200000022222000000002112222
c4	111011100200110001120210000000020022222
c5	111011100200111011122210100001121122222
c6	1111112100200111011122210100000121122222
c7	0001001200000011102112221011110112022222
No	8888888889999999
	123456789012345
c1	000202221012202
c2	001202220002202
c3	102202220002202
c4	001202220000100
c5	111202220001102
c6	011202220001102
c7	001202220001102

Parsimony analysis of gross-morphological position of prepattern centers

The prepattern centers were also coded according to their placement on either clavus or endocorium (between claval and median fractures) or exocorium (between a median fracture and a costal margin), on either proximal or median or distal part of the sclerotized part of the forewing (clavus + corium), and in either interanal or medio-cubital or subcosto-radial vein cells. The data matrix (Table 3) was analysed by Hennig86 (option ic*).

RESULTS AND DISCUSSION

Morphological organization of forewing coloration

Cuticular melanization vs. epidermal pigmentation

Diversity of the pyrrhocorid forewing coloration is caused by superposition of two, probably independently developed and evolved, patterns—the pteridine pigmentation of epidermis (Socha & Némec 1996; Porcar et al. 1996; Bel et al. 1997) and melanization of the cuticle. Epidermis thus determines all white, yellow, orange, red, and red-brown shadows, cuticle various shadows of brown to black (epidermal pigmentation is visible only through transparent, nonmelanized cuticle).

Larval wingpads are more or less uniformly dark, covered with uniformly melanized cuticle (Fig. 3A), and the complex color patterns are differentiating during adult metamorphosis. Developmental origin of the color pattern is thus very abrupt; its sequence may be visualized by genetic as well as epigenetic (JHA-treatment) disturbances (Socha 1984, 1985, 1987; Zrzavý 1995). Ontogeny of

Table 3. Gross-morphological position of prepattern centers. 1 – center on clavus, 2 – center on endocorium, 3 – center on exocorium, 4 – center in proximal part of the clavus + corium, 5 – center in distal part of the clavus + corium, 6 – center in median part of the clavus + corium, 7 – center in interanal field, 8 – center in medio-cubital field, 9 – center in subcosto-radial field

	1	2	3	4	5	6	7	8	9
c1	1	0	0	1	0	0	1	0	0
c2	1	0	0	0	0	1	1	0	0
c3	0	1	0	1	0	0	0	1	0
c4	0	1	0	0	1	0	0	1	0
c5	0	1	0	0	0	1	0	1	0
c6	0	0	1	0	0	1	0	0	1
c7	0	0	1	0	1	0	0	0	1

forewing epidermal pigmentation has never been analysed thoroughly because the pigmentation of larval wingpads is usually not visible.

Pattern vs. background, and structure of the background

Only dark areas which are at least in one species distinguished from the light background and from other dark areas are treated as *pattern* elements. However, also the other, *background*, areas may be darkened in some species, or they may display some distinct color gradients. For example, in *Dysdercus albofasciatus* Berg, 1878, the whole proximal part of the corium (a2 in Fig. 1B) is dark but median complex of pattern elements (c4+5+6 in Fig. 1C) is still distinct; in some *D. obscuratus* Distant, 1883, specimens, the median patterns are very light and can be distinguished from the similarly colored background by different sculpture ("... the dot is present structurally but without its black pigment": Doesburg 1968: 103). Diversity of pyrrhocorid coloration is then determined not only by differential activity of prepattern centers, but also by differential melanization of background areas; two wings with the same combination of active prepattern centers may not be similar to each other.

There are at least four forewing areas whose background melanization is determined independently (Fig. 1B):

- (a1) *Claval area* (clavus).
- (a2) *Basicorial area* (corium proximally to the median pattern excluding its costal margin).
- (a3) *Disticorial area* (corium distally to the median pattern excluding its costal margin).
- (a4) *Costal area* (costal margin of a corium, especially of its proximal part).

Structure of the pattern

There are seven prepattern centers on the forewing, as revealed by independent expression in various pyrrhocorid species (Table 1, Fig. 1C):

- (c1) *Basiclaval center*: in the proximalmost part of the clavus, between anal veins 1A and 2A (*Probergrothius* Kirkaldy, 1904; *Sericocoris* Karsch, 1892; perhaps also *Callibaphus* Stål, 1870), probably never extend distad.
- (c2) *Disticlaval center*: between 1A and 2A in the posteriormost angle of the clavus, sometimes probably extends proximad (*Antilochus* Stål, 1863; *Dysdercus* Guérin Méneville, 1831; *Roscius* Stål, 1866).
- (c3) *Basicorial center*: in the proximal part of the corium, posteriorly to M and median fracture, anteriorly to Cu (*Pyrrhocoris* Fallén, 1814; topology of the color pattern suggests its presence also in some dark species like *Roscius guilielmi* Bergroth, 1926).

Median centers (*c4* to *c6*) form a complex of median color-pattern elements, difficult to homologize. However, there are some species or even individuals enabling to interpret the median color pattern as a complex of three independent pattern-forming centers (cf. Doesburg, 1968: 45, 54, 70): *Dysdercus ruficollis* (Linnaeus, 1764), *D. ocreatus* (Say, 1832), *D. andreae* (Linnaeus, 1758), *D. concinnus* Stål, 1861, *Probergrothius sexpunctatus* (sometimes even asymmetric, with different coloration of individual wings in a single specimen).

(*c4*) *Posterior median center*: at distal margin of corium, between *M* and *Cu*, near to *M-Cu* membrane cell; independently expressed e.g. in *Dysdercus flavidus* Signoret, 1861, but usually fused with the other centers of the median complex (*c5*+*6*, *c5*).

(*c5*) *Central median center*: in the median part of corium, between *M* and *Cu*, posteriorly to median fracture; generally, it forms a spot fused with centers *c4* and/or *c6*.

(*c6*) *Anterior median center*: in the median part of corium, at or near to *R*, anteriorly to median fracture; usually it extends anteriad, reaching the costal margin of corium.

(*c7*) *Angular center*: between costal and distal margins of the corium; at *R* (*Probergrothius*) or, more frequently, between *R* and *Sc* (*Callibaphus* Stål, 1870, *Dindymus* Stål, 1861, and *Dysdercus* part.).

Co-development and coevolution of prepattern centers

Hierarchy of pattern-forming centers

The parsimony analysis of the pyrrhocorid forewing prepattern centers shows a single scheme (CI 0.77, RI 0.81) which connects two posterior-proximal centers (*c1*+*3*) with the disticlavial center (*c2*), and, on the other hand, two median centers (*c5*+*6*) with the angular center (*c7*) and then with the posterior median (*c4*) one (Fig. 2A). This cladogram is not morphologically trivial since the gross-morphological information concerning position of the individual pattern-forming centers on the

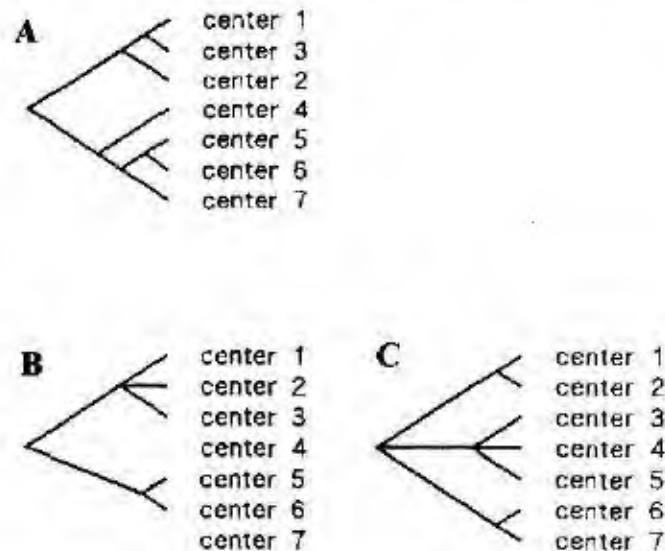


Fig. 2. Parsimonious hierarchies of the prepattern centers obtained from (A) pyrrhocorid comparative morphology; (B) developmental morphology of *P. apterus* and *D. cingulatus*; (C) gross-morphological characterization of centers' positions.

forewing (Table 3) provides different, incompatible, results (including components $c3+4+5+6+7$, $c3+4+5$, and $c6+7$; Fig. 2C). Consequently, the obtained hierarchy of the prepatter centers does not simply reflect their positions on the developing forewing but must be governed by some additional (epi)genetic mechanisms.

Individual variability of adult color patterns

(a) Individual variability of *P. apterus* is based predominantly on various melanization of background areas $a2$ and $a3$, especially of their endocorial parts. Spot $c3$ sometimes fuses with the claval melanization (similarly as in *Roscius guillelmi*), median spot $c5+6$ may exceptionally be antero-posteriorly fragmented by the median fracture (Henke 1924; R. Socha pers. comm.).

(b) *Probergrothius sexpunctatus* displays independent expression of both median centers, $c5$ and $c6$. They are usually fused into a single spot but they may be developed as two distinct spots, or one of them may be lacking.

(c) Many species of *Dysdercus* [e.g. *D. collaris* Blöte, 1931, *D. imitator* Blöte, 1931, *D. mimus* (Say, 1832), *D. flavolimbatus* Stål, 1861, *D. concinnus* Stål, 1861, *D. obscurus* Distant, 1883, *D. nimbatus* Hussey, 1929, *D. fulvipes* (De Geer, 1773), *D. maurus* Distant, 1901, *D. ruficollis* (Linnaeus, 1764); Doesburg 1968; Zrzavý & Nedvěd 1997] are highly variable. Usually they show (1) independent regulation of melanization of the pattern and background areas, (2) coupled regulation of almost all individual pattern centers (uniformly light and uniformly dark specimens often coexist), (3) complex structure of the median pattern displayed by its extreme variability, and (4) strong co-activity of median ($c4+5+6$) and angular ($c7$) centers.

Genetics of coloration

Most of mutations and strains of *P. apterus* affect body coloration but it is usually limited to changes of the epidermal pigments. Only *melanotic* (*m*), *unstable micropterism* (*ump*), and *red-dish lobes* (*rl*) [*rl(17)*] affect organization of the color patterns:

(a) *m* (Sláma 1998) is inherited as autosomal recessive and its phenotype effect consists in pronounced melanism of the wings and pronotum: the black spots as well as the distal dark margin of the corium are slightly broader and red background tends to be darker; sometimes, both corial spots are connected by a narrow stripe running along the median fracture. This mutation brings no information about organization of the color pattern and its function may be interpreted as simple change in the rate or timing of propagation of a signal that establishes spot boundary and/or in the threshold of response to this signal.

(b) *ump* is sex-linked recessive and genetically unstable; Socha (1993, 1995) speculated about its possible transposon-mediated origin. This mutation causes irregular reduction of the wings to micropterous condition, often asymmetric within a wing pair, together with corresponding distortion of color patterns. Similar modifications of color pattern were found in teratological micropterous specimens by Seidenstücker (1953).

(c) *rl(17)* strain was selected from a standard laboratory population: it contains specimens with the most adult-like coloration on L_5 wingpads but with the wildtype adult coloration (Socha 1984, 1985, 1987). This strain was found to be stable for many generations and not influenced by any external affects (photoperiod, JHA treatment). Genetic analyses show the *rl* trait(s) as polygenic and not linked to any of the genes affecting body coloration. The trait is interpreted as causing heterochronic shift of color-pattern differentiation to earlier stages, independently of stable timing of the gross morphogenesis of a wing. Putative "precociously metamorphosed individuals (PMI)", described by Socha (1987) within *rl(17)* strain, are evidently larvae with some further adult-like features especially in pronotal and abdominal coloration (but with larval wingpads, tarsi, scent glands, genitalia, and inner reproductive organs; Štys & Davidová-Vilimová 1989).

Development of P. apterus and D. cingulatus coloration

(a) Last larvae (L_5) of *P. apterus* usually have dark wingpads with light costal margins (about 75% of standard laboratory population; Socha 1984, 1985). From this stripe (= $a4$) the light area may extend posteriorly, usually in two tongues, proximal (= $a2$, not reaching future claval fracture) and distal (= $a3$, it encircles $c5+6$ remaining fused with distal melanization; Fig. 3A); there are also two small nonmelanized areas situated at tips of both tongues and developed primarily as independent of them. Levels of expression of proximal and distal tongues are independent [e. g. in *rl(17)* the distal tongue is significantly more developed; Fig. 3A]. Future claval fracture is usually not visible: there is a single posterior dark area, uniting fields situated both anteriorly and posteriorly to the claval fracture ($c1+2+3$ & $a1$). During the postecdysial melanization of freshly emerged L_6 larvae, future $c5+6$ spot is visible even in uniformly dark wildtype wingpads and is fused with the pad base by a narrow darker stripe (along posterior border of $a4$).

(b) Differentiation of individual pattern elements is not tightly coupled. In *rl(17)* strain of *P. apterus*, there is a high proportion of adults without the proximal spot ($c3$). Whereas differentiation of the median spot ($c5+6$) was shifted to L_5 - L_6 molting so that adult-like coloration appears in L_5 , $c3$ remains to be differentiated during metamorphosis but may not be developed at all. Substrain of *rl(17)* with secondarily stable presence of $c3$ was also selected (R. Socha unpubl.; Socha 1993: 247), without any influence on timing of the expression of $c5+6$. There are three types of individuals:

- (i) wildtype individuals: $c3$ (L_5 -Ad); $c5+6$ (L_5 -Ad),
- (ii) *rl(17)* individuals without $c3$: $c3$ (never); $c5+6$ (L_5 - L_6);
- (iii) *rl(17)* individuals with $c3$: $c3$ (L_5 -Ad); $c5+6$ (L_5 - L_6).

(c) Prothetic specimens of *P. apterus* (Fig. 3B) show that the median spot ($c5+6$) is restricted by extension of light costal stripe posteriad in the distal part of a wing (forming $a3$) and by origin of a

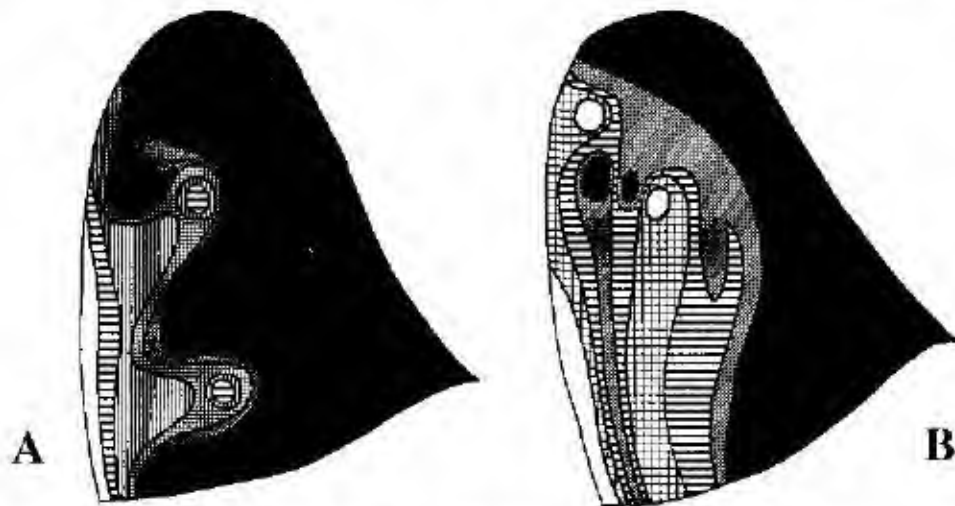


Fig. 3. Morphogenetic organization of color patterns of *P. apterus* (mapped on an idealized L_5 wingpad). (A) according to individual variability of L_5 lobes [wildtype: white areas are nonmelanized, *rl(17)* strain: white and hatched areas are nonmelanized]. (B) according to prothetic specimens. Contour lines and patterning indicate how individual fields tend to be melanized (from black = always melanized, to white = never melanized).

new light area forming a_2 , the median spot is connected with the wing base by a dark stripe running anteriorly to the median fracture. The claval fracture is sometimes marked by a light line posterior to a dark stripe running along Cu . The prothetelic individuals also tend to possess more or less melanized background (intermediate between dark L_1 and light adults).

(d) Young larvae (to L_4) of *D. cingulatus* have uniformly dark lobes (without light costal margin), L_5 larvae have nonmelanized background areas a_1 , a_2 , and proximal part of a_4 , the median spot (c_5+6) remains fused with dark distal part of a lobe (a_3 + membrane). (Similar adult coloration, with melanized $c_4+5+6+7$ & a_3 , parallelly evolved in *D. ruficollis*, *D. minus* + *D. imitator* + *D. bloeteri*, and *D. obscuratus*, according to Zrzavý & Nedvěd 1997). Prothetelic specimens of *D. cingulatus* tend to possess median spot fused with wing base by a dark stripe along the median fracture, and more or less melanized costal margin of a wing (a_4).

The following conclusions are possible:

- (i) Differentiation of the color pattern is independent of structural morphogenesis of a forewing. Timing of color-pattern development is not controlled by hormonal or environmental factors.
- (ii) Individual color-pattern centers are controlled independently. All pattern-forming centers may independently be subjected to developmental (and evolutionary) change.
- (iii) Both *rl(17)* and prothetelic specimens show compatible scenarios of color pattern differentiation (proximal-posterior complex c_1+2+3 vs. median complex c_5+6). The median spot is sometimes fused with more proximal elements (some aberrant adult wings, postecdysial melanization of L_5 lobes, some prothetelic specimens) and sometimes with more distal ones [some aberrant adult wings, some L_5 wingpads like *rl(17)*]. This is probably caused by its composite nature, some prothetelic specimens suggest that c_6 is an extension of the basal melanization of a lobe and c_5 of its distal melanization (Fig. 3B). Spots c_4 and c_7 cannot be classified since they are not expressed in the model species.

Conclusions

Both comparative and developmental morphology provide compatible results as concerns hierarchical relationships of the prepattern centers: c_1+2+3 vs. $c_4+5+6+7$ (comparative analysis) and c_1+2+3 vs. c_5+6 (developmental morphology). In both cases, the hierarchy is not compatible with that derived from adult structure of the wing (c_1+2 vs. c_3+4+5 vs. c_6+7). The pattern-determining system is probably determined earlier than the wing structure is differentiated and probably independently of it [as visualized by *rl(17)* specimens].

The generalized pyrrhocid color pattern (not necessarily but possibly the pyrrhocid ground-plan) is a light forewing with dark median pattern (spot or transversal stripe, c_4+5+6 , or some of them), it is often accompanied by the dark clavus (c_1+2 & a_1 , or some of them) and by the dark angular spot (c_7). So, there are three *topological*, hierarchy-independent, complexes of color-pattern centers forming three dark areas, which are isolated from each other by light background areas (Fig. 1). The complicated forewing coloration is then morphogenetically easy to evolve. Most species with the median spot possess also the angular spot because they both form a single morphogenetic unit.

Consequently, the general similarity of many pyrrhocid species is probably a mere consequence of the shared morphogenetic pathway. All animals with these pathways tend to response to similar adaptive regimes by evolving the same morphology. No adaptive convergence of the similar species (e.g. mimicry) must then be *a priori* expected, and more historical-ecological analyses are necessary to hypothesize the existence of mimicry rings (Zrzavý & Nedvěd 1999).

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- (f) Nikolajev G. V. 1987. *Plastinčatousye zhuki (Coleoptera, Scarabaeoidea) Kazakhstana i Srednej Azii [Scarabaeoidea (Coleoptera) of Kazakhstan and Central Asia]*. Alma-Ata: Izd. Nauka KazSSR, 232 pp. (in Russian).
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